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Local, regional, and global patterns of woodpecker (Picidae) diversity: ecological explanations and practical applications

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LOCAL, REGIONAL, AND GLOBAL PATTERNS OF WOODPECKER (PICIDAE) DIVERSITY: ECOLOGICAL EXPLANATIONS AND PRACTICAL APPLICATIONS

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ABSTRACT

This study explored foraging ecology in a guild of 13 woodpecker species found in the lowland rainforests of peninsular Malaysia. The data collected were used for two purposes: (1) to compare species from temperate and tropical woodpecker assemblages in an attempt to understand patterns of diversity, and (2) to determine the effects of logging on Malaysian woodpeckers.

Ecological and morphological patterns of diversity were investigated in woodpeckers from tropical sites in Malaysia (Pasoh Forest Reserve and Sungai Lalang Forest Reserve) and Guatemala, and two temperate sites in North America. Multivariate analyses separated species into two ecomorphs: "conventional" - species that excavated frequently and had large bills, long bracing tails, and relatively short toes, and "novel" - species that used a variety of microhabitats (bamboo, ant nests) and had relatively short tails, short, flattened bills, and long toes. Both temperate and tropical species were classified as the first ecomorph, but the "novel" ecomorph comprised primarily tropical species. These woodpeckers used tropical resources not readily available year-round in temperate forests, such as arboreal ant and termite nests, bamboo, and leaves. These novel resources may explain the maintenance of high woodpecker diversity in tropical rainforests.

Woodpecker response to logging exhibited some atypical patterns. Overall abundance in recently logged stands (mean = 5 years) is similar to unlogged forest, but drop by half in older stands (mean = 10 years). Numbers rebound in older (25 + years) stands, but species composition differs significantly from that in unlogged forest. The abundance of preferred microhabitats (particularly snags) also follows this pattern and suggests that the effects of logging are delayed for woodpeckers. Rainforests often incur massive damage during logging,

and many logs, stumps, and damaged trees are left behind. The result is a spike in necromass available to woodpeckers for foraging and nesting. This supply buffers woodpecker populations in the years immediately following logging, but as the dead wood decays, woodpecker numbers drop. Large, snag-foraging woodpeckers seem most affected in the long term. The importance of snags should be considered in the management of Malaysian forests.

CHAPTER 1
INTRODUCTION

This study attempts to answer two questions about woodpecker communities: (1) Why are there more species in tropical rainforests and (2) How are tropical woodpeckers affected by habitat disturbance? To answer these questions, a diverse assemblage of woodpeckers was studied in lowland Malaysian rainforests. I made foraging observations, conducted censuses, and surveyed important woodpecker microhabitats in logged and unlogged forest. Chapter 1 presents the data collected in the field, and Chapters 2 and 3 examined these questions within a broader context.

Part of Chapter 1 investigates the foraging ecology of 13 species of woodpecker most commonly found in lowland Malaysian rainforests. Diversity in the foraging ecology of these woodpeckers was considerable, but most species could be categorized into one of two groups based on microhabitat preferences: (1) birds that foraged on primarily on trees (live, dead, or dead parts of live trees), and (2) birds that used microhabitats not typically available year round in temperate forests (i.e., bamboo, leaves, rattan, lianas, and arboreal ant and termite nests). This pattern suggested that the exploitation of these "additional" resources explains, in part, the increased diversity of woodpeckers in Malaysian rainforests.

Chapter 2 investigates this idea further by comparing the data collected in Malaysia to another set of comparative woodpecker ecological data from Guatemala, Maryland, and Minnesota. By correlating ecology with morphology, the characterization of a distinct "novel" ecomorph emerged from the data sets. I then studied the morphology of species in seven woodpecker assemblages from around the world in an attempt to identify this tropical ecomorph in temperate and tropical assemblages from a variety of locations.

Part of Chapter 1 also presents results from line-transect surveys and microhabitat sampling in primary forest and logged stands of various ages. Logging affected species in different ways, but an intermediate-age stand (10- years-old) had low abundance of all species. Microhabitat sampling revealed a lack of snags in these intermediate stands, and use vs. availability profiles revealed that snags were used with much higher frequency than their availability would predict in all forest types. These results indicated that snags may be an important consideration in the management of Malaysian forests.

Chapter 3 summarizes the results of Chapters 1 and 2. It also includes a review of the studies of logging in Southeast Asia and the larger issues of habitat fragmentation and conversion of forest to plantation. This review addresses the role of forest management to conservation and the importance of sustainable management in preventing conversion, fragmentation, and the related loss of rainforest species.

CHAPTER 2
FORAGING ECOLOGY OF WOODPECKERS IN SELECTIVELY LOGGED LOWLAND RAINFORESTS IN PENINSULAR MALAYSIA: THE RELATIONSHIP BETWEEN RESOURCE AVAILABILITY AND WOODPECKER ABUNDANCE

Introduction

Lowland rainforests of Southeast Asia are unique in having the highest single-point diversity for woodpeckers (Picidae) in the world (Short 1978, Styring and Ickes 2001, Wells 1999). With up to 16 species in a single patch of habitat, woodpeckers comprise the majority of the bark-foraging guild in this region and a larger percentage of the total avifauna than do woodpeckers in other tropical forests (6-8 % of total species versus 3–5% and 2–3% for tropical rainforests in the Neotropics and Africa respectively; see Styring and Ickes 2001). A variety of genera and a broad range of body sizes are represented in this Southeast Asian guild (Table 1.1).

Table 1.1. List of the 13 woodpecker species commonly found in lowland rainforests in Malaysia. Mean weights taken from Short (1978).

Species	English Name	Species Code	Mean Mass (g)
Sasia abnormis	Rufous Piculet	**SA**	9
Hemicircus concretus	Grey-and-Buff Woodpecker	**HC**	32
Meiglyptes tristis	Buff-rumped Woodpecker	**MT**	46
Meiglyptes tukki	Buff-necked Woodpecker	**MTU**	53
Celeus brachyurus	Rufous Woodpecker	**CB**	66
Blythipicus rubiginosus	Maroon Woodpecker	**BR**	84
Picus puniceus	Crimson-winged Woodpecker	**PP**	98
Picus mentalis	Checker-throated Woodpecker	**PM**	89
Picus miniaceus	Banded Woodpecker	**PMI**	83
Dinopium rafflesii	Olive-backed Woodpecker	**DR**	96
Reinwardtipicus validus	Orange-backed Woodpecker	**RV**	155
Dryocopus javensis	White-bellied Woodpecker	**DJ**	225
Mulleripicus pulverulentus	Great Slaty Woodpecker	**MP**	430

Woodpeckers are highly adapted for excavating woody substrates to obtain food and nesting space, and they form a discrete ecological guild in forests where they occur. Understanding how so many ecologically similar species can coexist within one forest will provide insight into resource use and potential resource partitioning, and can help us understand

how this guild responds to disturbance. Short (1978) qualitatively described the foraging and nesting behavior of 13 woodpecker species at Pasoh Forest Reserve and several other sites in Peninsular Malaysia. Although quantitative data on foraging were lacking, his observations suggested that woodpeckers partitioned resources behaviorally by using a variety of foraging methods, foraging heights, and substrates. We approached the hypothesis of niche differentiation by making detailed, quantitative observations on the foraging ecology of 13 species at Pasoh Forest Reserve (PFR) and Sungai Lalang Forest Reserve (SLFR).

The rainforests in Southeast Asia are being logged for timber at such a rapid rate that understanding the effects of logging on plant and animal species in these forests is timely and imperative. Although selective logging for timber is often considered sustainable, the long term effects of selective logging on plant and animal communities are not well known (Johns 1988, Vincent 1995). Effects are also likely to vary depending on harvest limits and damage caused by extraction techniques. Studies of bird communities in peninsular Malaysia and Borneo as well as other tropical locations indicate that bird diversity and species composition are affected by selective logging (Aleixo 1999, Johns 1989, Johns 1996, Lambert 1992, Wong 1985), with some understory insectivores disappearing or becoming rare and edge species penetrating the interior of logged stands and increasing in abundance.

Woodpeckers are often considered particularly sensitive to logging because most species excavate nest cavities in trees and many forage on dead wood. Studies of rare or endangered woodpeckers often indicate that these species need a substantial number of mature, "overmature," or dead and dying trees upon which to forage or excavate cavities (Allen and Kellogg 1937, Collar et al. 1994, Dennis 1948, Greenway 1967, Hanula & Franzreb 1998, Jackson et al. 1979, Nelson 1898, Tanner 1942, Tanner 1964). In temperate regions, studies

indicate that snags (standing dead trees) are less common in logged forest compared to unlogged or old growth forest (Rosenberg et al. 1988). Research in the tropics indicates that snags may be less common at lower latitudes (Gibbs et al. 1993) and that tree cavities are less common in logged compared to unlogged tropical forest (Pattanavibool and Edge 1996). Given the importance of large trees and snags to the feeding and nesting biology of woodpeckers, this family of birds potentially is more susceptible to habitat degradation following logging than other groups.

Several studies have investigated the effects of selective logging on bird communities in both Peninsular Malaysia and Borneo and have provided evidence that woodpeckers may indeed be sensitive to logging (Johns 1989, Lambert 1992, Wong 1985). However, these studies lacked sufficient data to identify the most affected woodpecker species and focused on logged stands less than 25 years old. Investigating older managed stands is important, however, because many physical characteristics of logged forests change over time. For example, at least one study in a temperate latitude managed forest has shown that snags are decreasingly abundant in managed stands through time (Moorman et al. 1999), and others have shown that some woodpecker species may be negatively affected (Flemming et al. 1999, Virkkala et al. 1993).

Three goals were addressed in this study. First, to describe the diversity in foraging ecology of this species-rich guild, foraging observations of 13 species of woodpeckers were collected and analyzed. Second, to document the effects of logging on woodpecker abundance and diversity, woodpecker abundance and density in unlogged forest and logged forests of various ages were quantified. Third, to understand the relationship between woodpecker abundance and microhabitat availability among forest types, the availability of microhabitat at SLFR was quantified.

Study Areas

Research was conducted at two forest reserves in West Malaysia: Pasoh Forest Reserve (PFR) in the state of Negeri Sembilan (2º 59' N, 102º 17' E; May – July 1998), and Sungai Lalang Forest Reserve (SLFR) in the state of Selangor (3° 30' N, 101° 53' E; July – Sept. 1999, Feb. – April 2000, and June – Aug. 2000) (Figure 1.1a - c.). PFR consists of a core area of ca. 600 ha of virgin lowland dipterocarp forest and is surrounded by ca. 1400 hectares of forest that was selectively logged from 1955 to 1956 (Kochummen et al. 1990, Wong 1985, 1986) (Figure 1.1b.). Additional forest management techniques, such as poison-girdling of emergent non-commercial timber species and removal of climbers (lianas and rattans), were performed in the selectively logged portion of Pasoh between 1955 and 1960 (Kochummen et al. 1990). The forest is classified as lowland rainforest (elevation: 75-150 m, average annual rainfall: 1900 mm), and the emergent vegetation layer is dominated by various species in the Dipterocarpaceae, primarily in the genera *Shorea* and *Dipterocarpus* (Kochummen et al. 1990).

SLFR is a large forest reserve (17,722 ha), consisting of both recently logged (<5 year ago), mature forest logged as long ago as the 1940s (Figure 1.1c.), and a few patches of primary forest. The forest is classified as lowland/hill rainforest (elevation: 100-800 m, average annual rainfall: 3115 mm), and, like PFR, the emergent vegetation layer is dominated by species in the genera *Shorea* and *Dipterocarpus* (Laidlaw 2000). Data were collected at three sites within the reserve: Compartment 18 (5-year-old logged forest), Compartment 33 (10-year-old logged forest), and a patch of unlogged forest in Compartment 24 called a Virgin Jungle Reserve (VJR). Compartment 18, SLFR (260 ha) was logged from November 1993 to September 1995. Because data collection began in 1999 and ended in 2000, the forest is considered 5-year-old logged

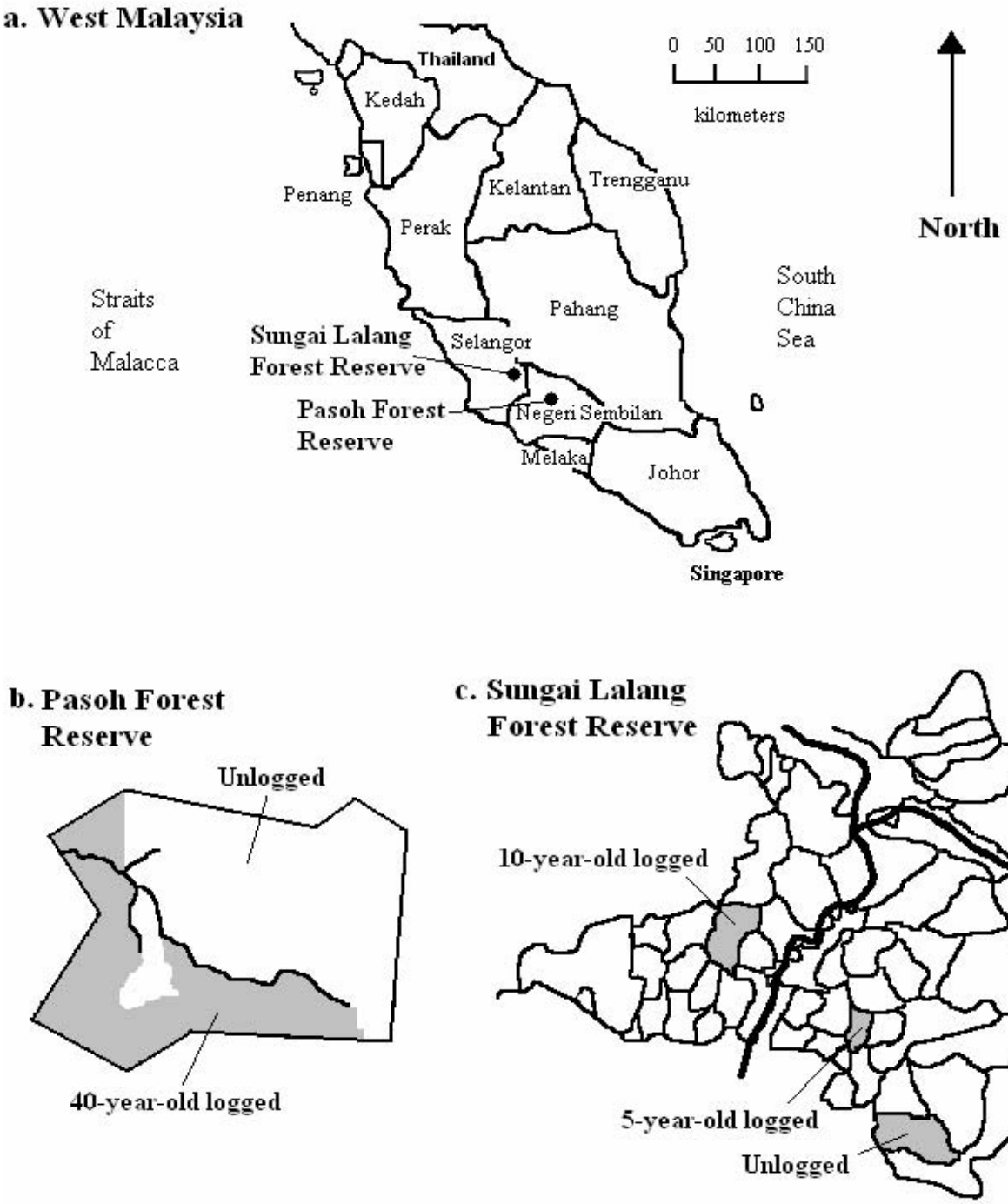


Figure 1.1. Maps of study sites.

forest. In all, 38,223 m^3 of timber were removed from the forest (136 m^3 ha^{-1} or about 16 trees ha^{-1}) and 3.5 km of logging roads (13.5 m ha^{-1}) were constructed. The forest at Compartment 18 appeared highly disturbed, but foraging resources such as residual large stumps, snags, and logs were abundant.

Compartment 33, SLFR (387 ha) was logged from January 1990 to March 1991 and is referred to as 10-year-old logged forest. The cutting limit was more restricted for this compartment (55-60 cm dbh) and although more timber was removed (26944 m^3), per capita removal was lower (96 m^3 ha^{-1}). However, more roads were built (18.6 km logging roads equaling 48 m of roads ha^{-1}). Because data on the length and number of skid trails was not recorded, it is hard to know how much damage occurred due simply to access for timber removal. The forest in this compartment looked much more like primary forest structurally, but certain resources such as snags and logs seemed low in abundance.

The third site at SLFR was a patch of unlogged forest (82 ha) located within a logged compartment (compartment 24 logged from 1960 to 1963). This unlogged patch of forest was designated as a protected area known as a Virgin Jungle Reserve (VJR). These reserves are designated in logging concessions throughout peninsular Malaysia and are meant to preserve sensitive wildlife species. Trees in the VJR are very large in girth and height, and large snags seemed abundant.

Methods

Foraging Observations

Throughout this study, ARS recorded the following data with a microcassette recorder on foraging birds encountered opportunistically: (1) estimated height above ground, (2) estimated distance from the canopy, (3) diameter at breast height (dbh) of the foraging substrate, (4) perch

diameter, (5) attack method ('chisel', 'flake', 'glean', 'hang', 'peck', 'probe'; Table 1.2), (6) horizontal placement (inner = trunk, middle = large branches, outer = branchlets/leaves), and (7) microhabitat ('ant/termite' – tunnels and nests found on the external surfaces of tree trunks and branches, 'bamboo', 'log' – a dead tree lying on the ground, 'liana' – a woody vine, 'dead patch' – a section of dead wood on a live tree, 'live wood', 'leaf', '*Macaranga*' – primarily *Macaranga gigantea* - a type of tree known to have mutualistic associations with ants, and 'snag' – a standing dead tree). All observations collected at PFR were made in primary forest, whereas observations were collected in both primary and logged forest at SLFR. Birds were followed for as long as possible, but only the initial observation was used for statistical analysis to avoid problems with non-independent data.

Multivariate analyses on foraging data reduced the information into a few, readily interpretable variables or vectors. Both continuous and categorical data were collected. Continuous variables were converted into categorical variables by using size and height classes. SYSTAT 8.0 (SPSS Inc.1998) was used to perform Principal Components Analysis on continuous variables (listed 1 – 4 in the previous paragraph). Principal Components Analysis reduces data by forming linear combinations of variables and is also useful in classifying variables. Analyses of variance and pair-wise comparisons of continuous variables were performed to determine natural 'breaks' in the data and thus meaningful categories.

Once continuous variables were converted to categorical frequency data, correspondence analysis was performed on the data set with SAS 8.00. Correspondence analysis is an ordination technique similar to principal components analysis, but it is effective at identifying structure in categorical frequency data by detecting correspondence between rows and columns of a data

matrix. Correspondence analysis extracted more variation in foraging data than other multivariate techniques (Miles 1990).

To determine which parameters were most important in distinguishing species, dissimilarity matrices were constructed for individual foraging parameters (perch, microhabitat, method, height, horizontal position) using SYSTAT 8.0 (SPSS Inc. 1998). These indices were combined to form an additive index of dissimilarity for each pair of species and an additive tree was built. Values of dissimilarity were calculated at every branch for each parameter so that the parameter accounting for the majority of dissimilarity at each branch could be determined.

Table 1.2. Description of attack variables used in this study (taken from Remsen and Robinson 1990).

Maneuver	Purpose
Glean	To pick food from a nearby substrate. Can be reached without full extension of legs or neck without the involvement of acrobatic movements.
Hang-down	To hang, head down in order to reach food not obtainable by any other perched position.
Reach-out	To reach laterally by extending legs and neck. Used to pick prey from nearby leaves.
Probe	To insert bill into cracks, holes, or soft substrates to capture hidden food.
Flake	To brush aside loose substrate with a sideways, sweeping motion.
Peck	To drive the bill against a substrate to remove some of the exterior of the substrate.
Chisel	Like "peck" but the bill is aimed obliquely rather than perpendicularly at the substrate.
Hammer	To deliver a series of pecks. Used to excavate deep holes to reach bark or wood-dwelling insects or sap.

Woodpecker Surveys in Logged and Unlogged Forest

Four kilometers of transects were used for surveys in each forest type at each site. At PFR, four trails 1 km in length were already established within the primary forest. In the logged forest, one 2-km and one 1-km trail were already established. Two additional trails were cut (436 m, and 564 m respectively) to bring the total distance to 4 km. At SLFR, transects were

already established in each forest type by researchers conducting a multifaceted study on forest recovery. The total length of established transects in each forest type at SLFR was roughly proportional to the size of the compartment (6.4 km, 7.1 km, and 4.4 km in the 5-year-old, 10-year-old, and unlogged forest respectively). However, only 4 km of transect were used (four 1-km transects) in each forest type for this study. To reduce repetition in counting woodpeckers, all transects were placed a minimum of 100 meters apart at PFR and SLFR. All forest types were either directly adjacent to one another (PFR), or were separated by a continuous matrix of forested habitat (SLFR), and woodpeckers, like most birds, are relatively mobile, and could potentially move between transects both within and between forest types. To minimize the effects of this problem no transect was walked more than once in any four-day period. In doing this we hoped to avoid counting woodpeckers that were only moving through an area more than once on a transect.

Surveys were conducted at dawn and dusk at PFR and at dawn only at SLFR. Each transect was walked six times: three times in the morning and three times in the afternoon at PFR (total of 48 surveys) and six times in the morning at SLFR (total of 72 surveys). Transects were surveyed slowly, at a rate of about 0.5 - 0.6 km / hour. At PFR attempts were made to locate visually every woodpecker detected and to measure their perpendicular distance from the transect with a 50-m tape. Birds that could not be located visually were included in the data, but recorded as "heard only". Because of the steep slippery terrain at SLFR, measuring distance with 50 –m tape was not feasible, so all birds seen or heard were recorded and their distance estimated by the observer.

Because the topographic differences between PFR and SLFR warranted slight differences in data collection and perhaps detection capability, census data were analyzed separately for each

site. Density estimates were also calculated with the program DISTANCE 3.5 (Thomas et al. 1998). Only overall woodpecker density was estimated due to low sample size for individual species. For this, and numerous other reasons, the density estimates probably are probably not accurate. However, because DISTANCE controls for differences in detectability in different habitats (based on the distribution of estimated distances from the transect), it allows comparisons to be more meaningful than raw abundances. Because more error is likely involved in estimations from SLFR than those from PFR, these data were analyzed as both exact distances and as bands (distance groupings, e.g. 0-10 m, 10-20 m, etc.) and the most conservative density estimate taken.

Microhabitat Availability

To determine if the relative abundance of woodpeckers correlated roughly with the abundance of preferred microhabitats, microhabitats commonly used by woodpeckers were quantified at SLFR. In each forest type, researchers studying floristic aspects of forest recovery established three one-hectare plots separated by a distance of roughly 100 m. Each one ha plot was divided into 100 10 x 10 m subplots. In each forest type, 100 subplots were randomly sampled among the three ha of plots for the following substrate variables: arboreal ant and termite nests, snags, logs, dead wood patches, and dead lianas. In each 10 x 10 m subplot every tree, log, and liana was scanned carefully with binoculars, and every 'woodpecker' substrate seen was documented and its width/diameter, length, and height above ground measured.

To determine if a microhabitat was used preferentially in respect to its abundance, use vs. availability profiles were constructed for individual species and forest types. Use vs. availability was calculated by subtracting the proportional availability of a given substrate (in comparison to the other substrates sampled) from their proportional use.

Results

Foraging Observations

Over the course of the study, 501 independent foraging observations was recorded. With the exception of *Meiglyptes tristis*, the number of foraging observations for individual species was rather low. Because there were only six observations of *Picus miniaceus*, this species was not included in any analyses. With only 10 independent observations, *Dinopium rafflesii* was included in some of the multivariate analyses, but not in analyses where probabilities were important.

Principal components analysis revealed two principal components that explained 82% of the variation in the data (Figure 1.2). Principal component one, which explained over 50% of the variation in the data set, was weighted heavily on perch diameter. Principal component two (explaining 30% of the variation in the data) was a combination of the variables 'height above ground' and 'distance from the canopy' and can be thought of as vertical placement. Based on principal components analysis and analyses of variance (Figure 1.2), 'perch diameter' was divided into 5 categories: XS – perch is less than 5 cm diameter, S – perch is 5 cm or greater and less than 10 cm, M – perch is 10 cm or greater and less than 20 cm, L – perch is 20 cm or greater and less than 35 cm, and XL – perch is greater than 35 cm. Likewise, 'vertical placement' was categorized into three categories: (1) understory – 5 m or lower, (2) midstory – higher than 5 m and lower than 5 m from the canopy, and (3) canopy – 5 m from the canopy or higher.

Although broad interpretations of the raw categorical data are not easily made, a few trends were apparent from the frequency data (Table 1.3; Figure 1.3). Substrates and attack methods varied considerably. However, all species used dead and live wood to some extent. The substrate variables '*Macaranga*' and 'leaf', and the method 'hang' were used by only three

species. *Meiglyptes tristis* used *Macaranga* extensively, and it often foraged on the tips of the branches of this tree, where the large leaves are.

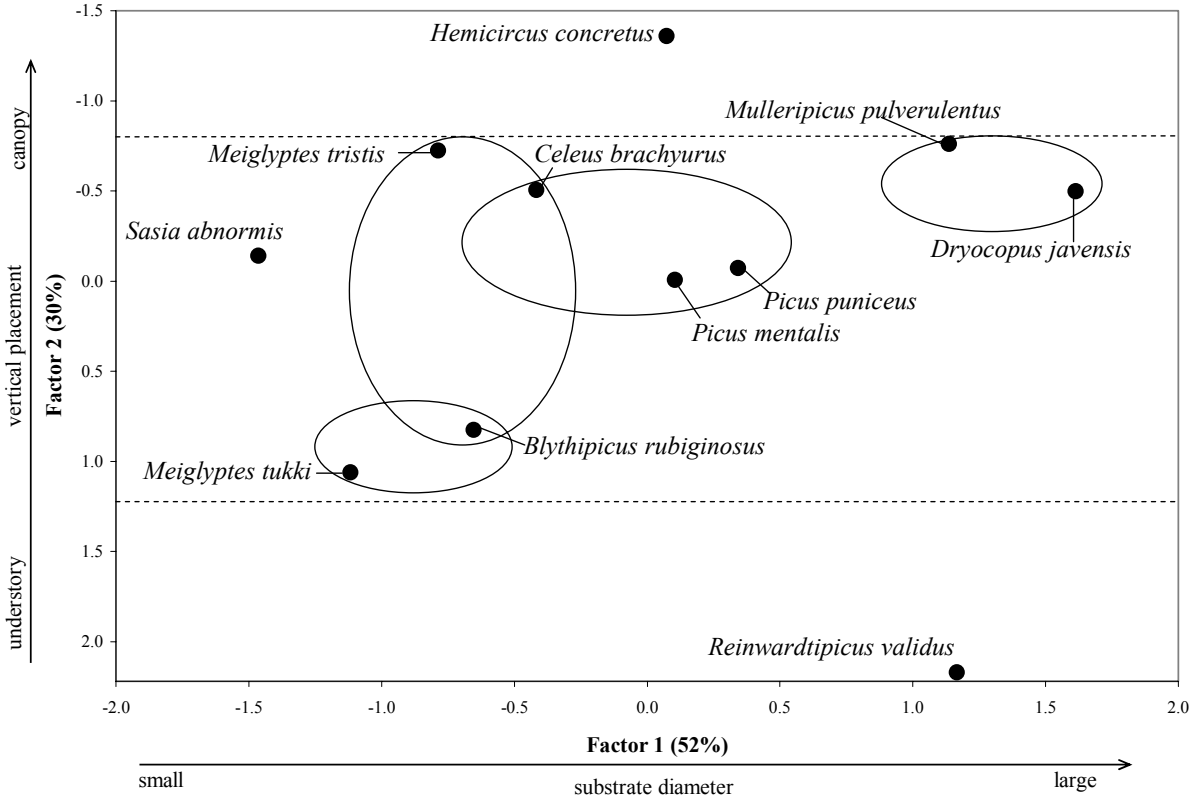


Figure 1.2. Principal Components Analysis of continuous foraging variables (perch diameter, DBH of foraging substrate, height above ground, and distance from the canopy. Circles indicate groups of species that did not differ significantly (probability of 0.05 or less) for any continuous variable when ANOVA was performed and pairwise comparisons made.

Correspondence analysis of foraging variables resulted in three dimensions that explained 52% of the variation in the data (Figure 1.4). Similar to the Principal Components Analysis, dimension one was weighted heavily toward perch diameter (followed by substrate). Dimension two was weighted heavily on the parameter substrate (followed by height). *Meiglyptes tristis,* which foraged primarily on leaves, and *Blythipicus rubiginosus,* which was restricted to dense understory, clearly separated from the other species. Also, the group containing the species

Table 1.3 a-c. Ecological variables used to perform correspondence analysis (CA). Data are written as proportions.
a. spatial variables

	Perch diameter					Height		Horizontal Position			
Species	**XS**	**S**	**M**	**L**	**XL**	**Under-story**	**Mid-story**	**Canopy**	**Inner**	**Middle**	**Outer**
Sasia abnormis	0.70	0.30	0.00	0.00	0.00	0.53	0.200	0.28	0.70	0.25	0.05
Hemicircus concretus	0.26	0.69	0.03	0.03	0.00	0.03	0.211	0.76	0.21	0.63	0.16
Meiglyptes tristis	0.28	0.58	0.10	0.00	0.04	0.159	0.42	0.42	0.14	0.29	0.57
Meiglyptes tukki	0.32	0.42	0.13	0.10	0.03	0.387	0.32	0.29	0.65	0.36	0.00
Celeus brachyurus	0.05	0.32	0.55	0.00	0.09	0.045	0.41	0.55	0.41	0.41	0.18
Blythipicus rubiginosus	0.00	0.29	0.47	0.06	0.18	0.647	0.29	0.06	0.88	0.12	0.00
Picus mentalis	0.02	0.14	0.43	0.18	0.24	0.058	0.71	0.23	0.76	0.19	0.05
Picus miniaceus	0.00	0.25	0.75	0.00	0.00	1.000	0.00	0.00	1.00	0.00	0.00
Picus puniceus	0.00	0.09	0.38	0.41	0.12	0.108	0.51	0.38	0.68	0.32	0.00
Dinopium rafflesii	0.00	0.33	0.67	0.00	0.00	0.100	0.70	0.20	0.30	0.70	0.00
Reinwardtipicus validus	0.00	0.06	0.12	0.33	0.49	0.151	0.64	0.21	0.83	0.13	0.04
Dryocopus javensis	0.00	0.00	0.03	0.36	0.61	0.028	0.36	0.61	0.64	0.36	0.00
Mulleripicus pulverulentus	0.00	0.00	0.45	0.03	0.52	0.000	0.41	0.59	0.45	0.52	0.03

b. microhabitat variables

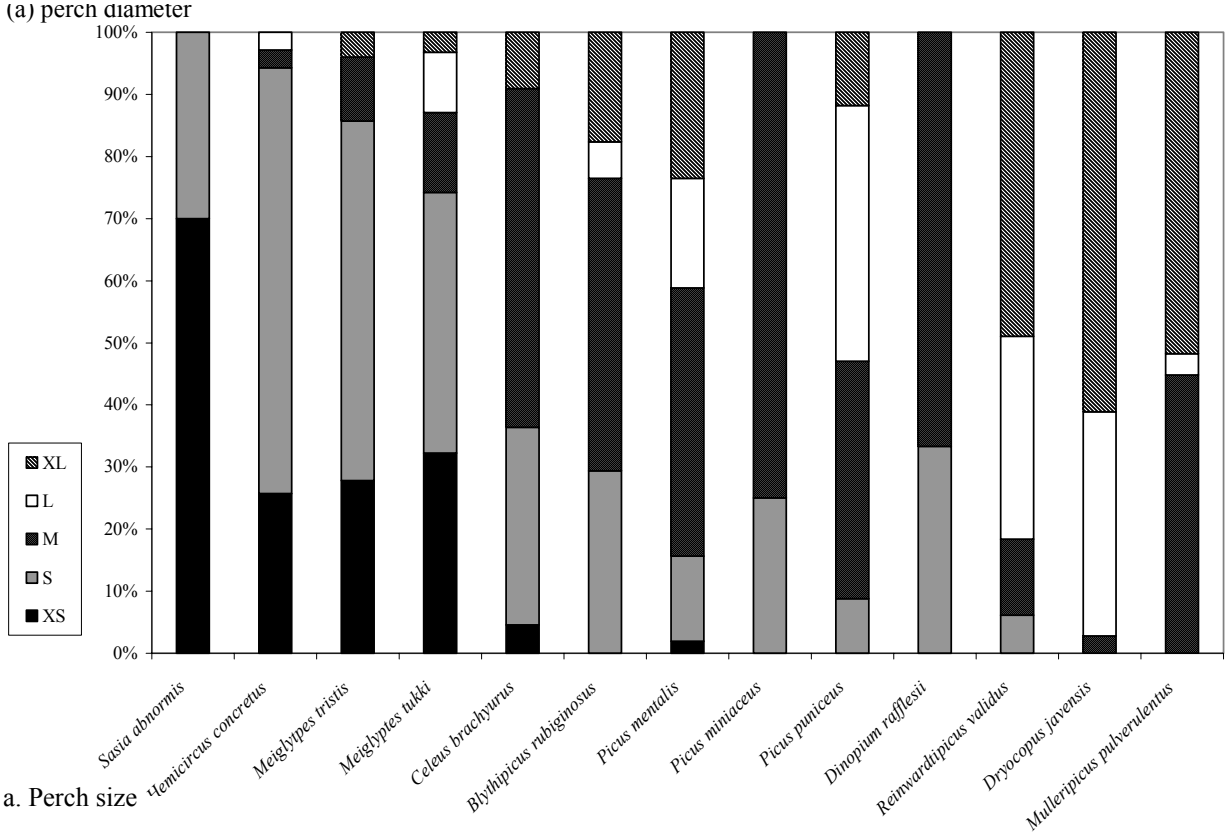
	Substrate									
	Ant/ Termite	**Bamboo**	**Log**	**Liana**	**Dead Patch**	**Live Wood**	**Leaf**	***Macaranga***	**Snag**	**Misc.**
Sasia abnormis	0.03	0.23	0.00	0.03	0.18	0.50	0.05	0.00	0.00	0.00
Hemicircus concretus	0.00	0.05	0.03	0.00	0.26	0.58	0.00	0.00	0.00	0.08
Meiglyptes tristis	0.16	0.03	0.00	0.02	0.06	0.15	0.14	0.42	0.02	0.00
Meiglyptes tukki	0.42	0.00	0.00	0.00	0.13	0.29	0.00	0.03	0.10	0.03
Celeus brachyurus	0.18	0.18	0.00	0.00	0.14	0.27	0.00	0.09	0.14	0.00
Blythipicus rubiginosus	0.00	0.00	0.35	0.12	0.06	0.24	0.00	0.00	0.18	0.06
Picus mentalis	0.03	0.02	0.00	0.02	0.57	0.29	0.00	0.00	0.05	0.02
Picus miniaceus	0.25	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.50	0.00
Picus puniceus	0.00	0.00	0.00	0.00	0.58	0.34	0.00	0.00	0.08	0.00
Dinopium rafflesii	0.00	0.10	0.00	0.00	0.50	0.30	0.00	0.00	0.10	0.00
Reinwardtipicus validus	0.00	0.00	0.00	0.04	0.12	0.04	0.00	0.00	0.79	0.02
Dryocopus javensis	0.00	0.00	0.00	0.00	0.14	0.06	0.00	0.00	0.81	0.00
Mulleripicus pulverulentus	0.00	0.00	0.00	0.00	0.24	0.35	0.00	0.00	0.41	0.00

(continued)

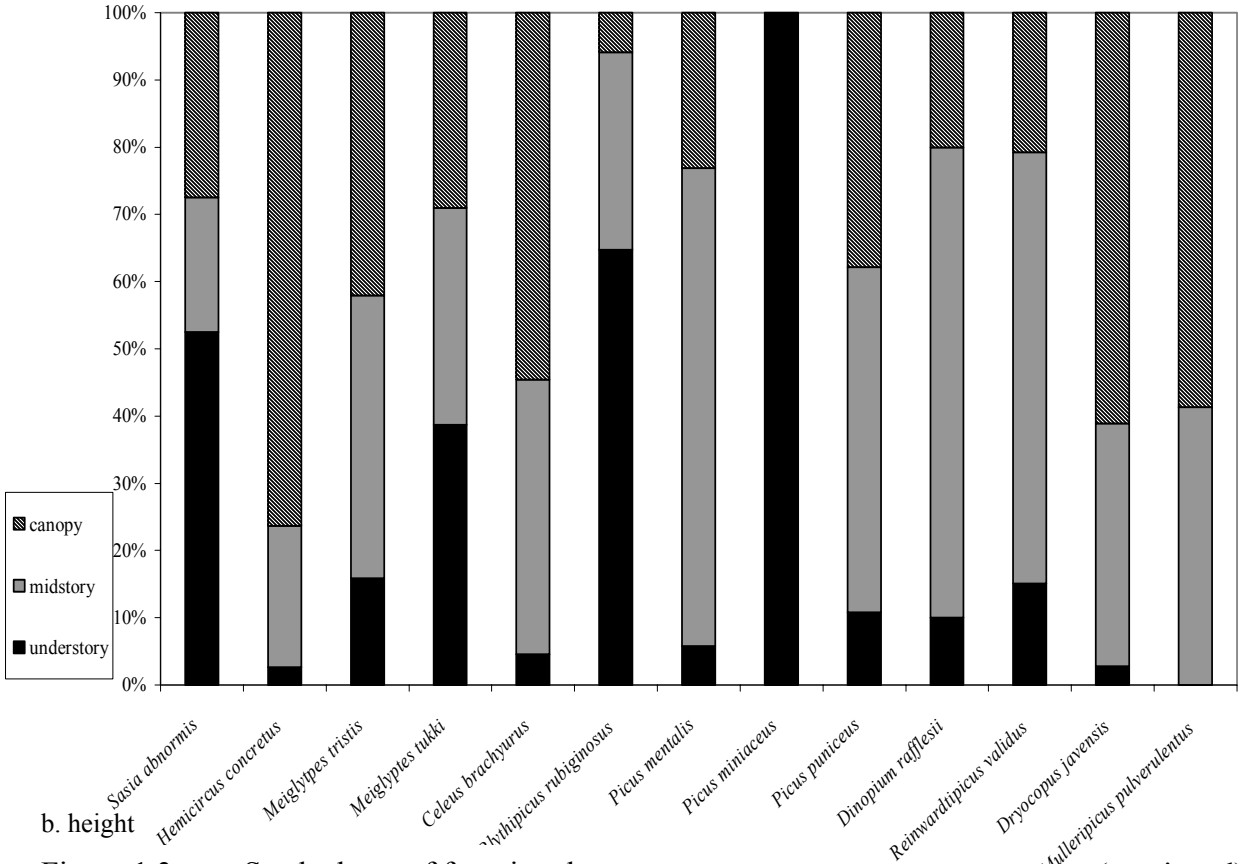
c. attack maneuver

	Attack maneuver							
	Chisel	**Flake**	**Glean**	**Hammer**	**Hang**	**Peck**	**Probe**	**N**
Sasia abnormis	0.00	0.00	0.20	0.50	0.00	0.30	0.00	40
Hemicircus concretus	0.00	0.00	0.26	0.50	0.08	0.08	0.08	38
Meiglyptes tristis	0.01	0.18	0.24	0.10	0.10	0.12	0.25	126
Meiglyptes tukki	0.03	0.00	0.23	0.26	0.00	0.48	0.00	31
Celeus brachyurus	0.05	0.14	0.55	0.05	0.05	0.18	0.00	22
Blythipicus rubiginosus	0.00	0.06	0.00	0.35	0.00	0.18	0.41	17
Picus mentalis	0.02	0.02	0.19	0.21	0.00	0.17	0.40	58
Picus miniaceus	0.00	0.00	0.00	0.00	0.00	0.50	0.50	4
Picus puniceus	0.08	0.03	0.08	0.32	0.00	0.40	0.11	38
Dinopium rafflesii	0.00	0.00	0.00	0.50	0.00	0.50	0.00	10
Reinwardtipicus validus	0.33	0.04	0.00	0.35	0.00	0.24	0.04	54
Dryocopus javensis	0.03	0.11	0.03	0.61	0.00	0.19	0.03	36
Mulleripicus pulverulentus	0.03	0.03	0.00	0.17	0.00	0.62	0.14	29

(a) perch diameter

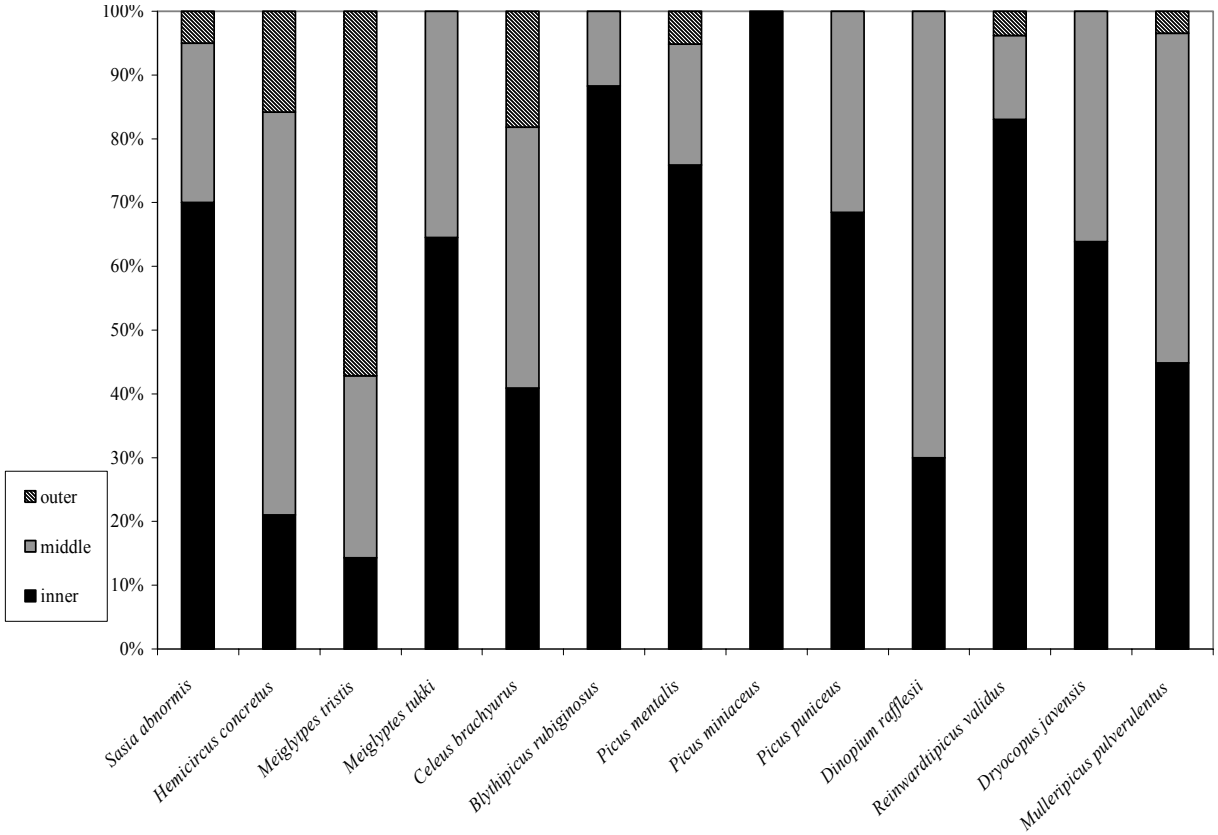


a. Perch size

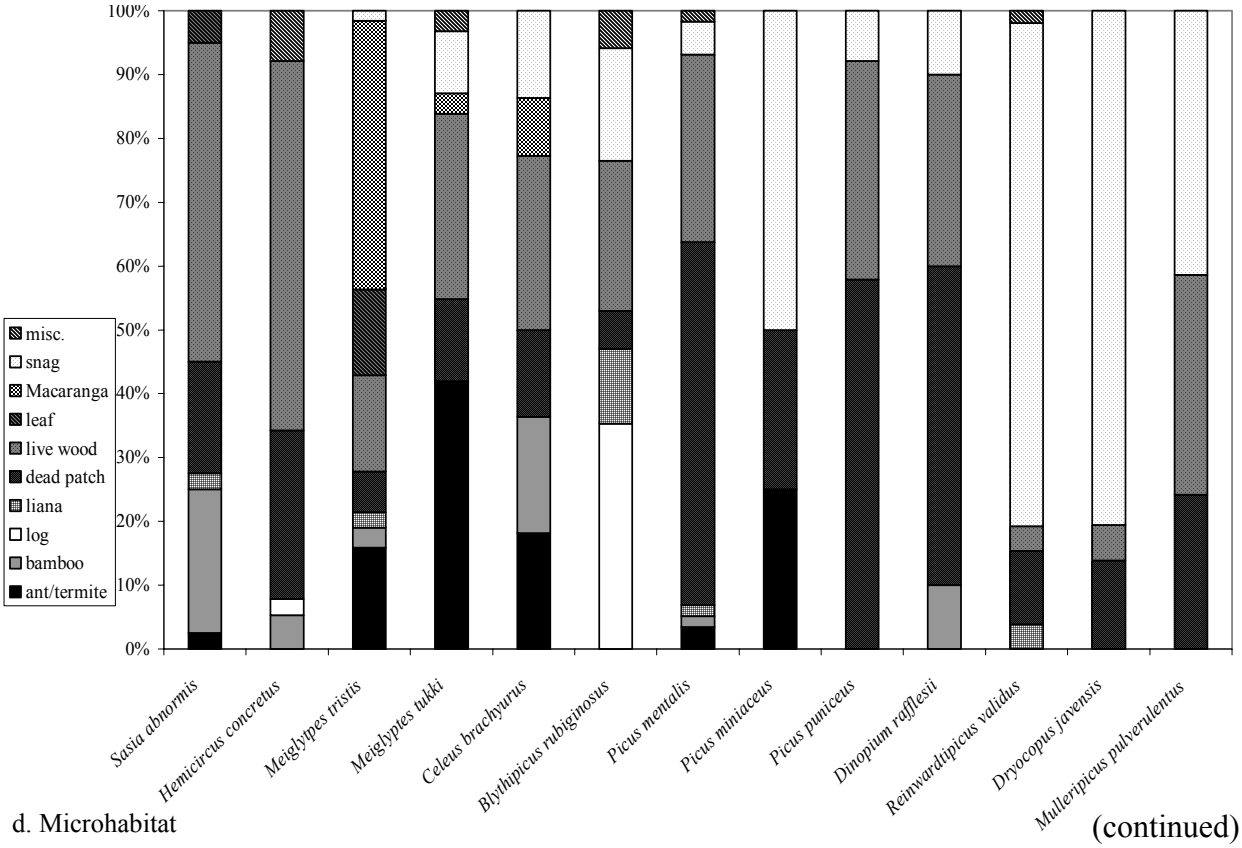


b. height

Figure 1.3 a-e. Stack charts of foraging data. (continued)

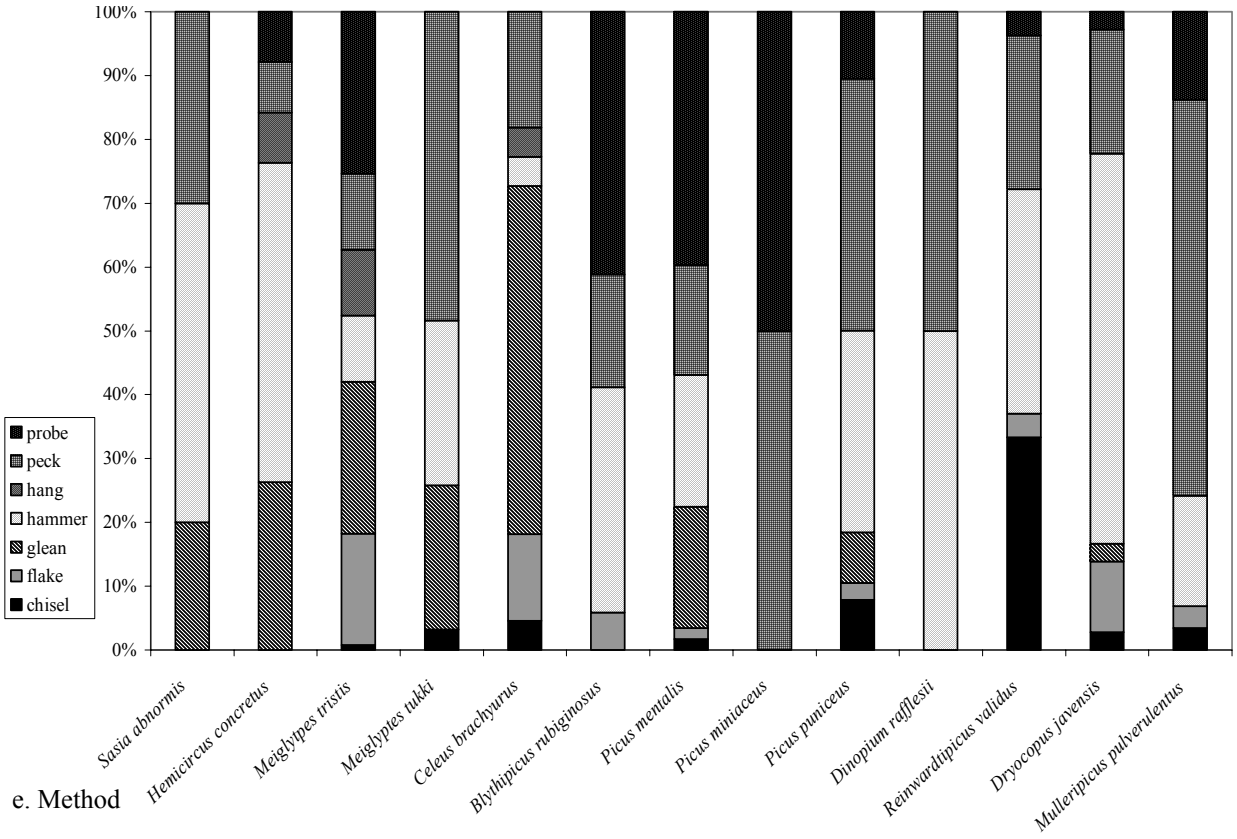


c. Horizontal placement



d. Microhabitat

(continued)



e. Method

Meiglyptes tukki, *Celeus brachyurus*, *Sasia abnormis*, and *Hemicircus concretus* (all of which used relatively small perches) was distinct from the group containing *Reinwardtipicus validus, Dryocopus javensis, Mulleripicus pulverulentus, Picus mentalis,* and *Picus puniceus* (which used larger perches).

The additive ecological tree built from the dissimilarity matrix revealed that perch diameter was important at the base of the tree and divided birds that used small perches from those that used large ones (Figure 1.5 and Table 1.4). Consequently, this division also represents birds that foraged on dead wood patches and snags (large perch birds) and birds that used more exclusively "novel" resources such as ant/termite nests and bamboo (small perch birds). At the next set of branches, each group was subdivided into more specific groups based on substrate preferences such as use of woody, live substrates including bamboo/small live branches and

Macaranga trees (*Meiglyptes tristis*, *Celeus brachyurus*, *Sasia abnormis* and *Hemicircus concretus*) vs. use of from those who used arboreal ant nests (*Meiglyptes tukki*); and dead liana/rattan (*Blythipicus rubiginosus*) vs. use of dead wood patches (*Picus mentalis* and *P. puniceus*) and snags (*Reinwardtipicus validus*, *Dryocopus javensis*, *Mulleripicus pulverulentus*). At the terminal branches, behavioral variables such as vertical placement and foraging method were useful in separating individual species. The only exception to this pattern of subdivision is the species pair *Celeus brachyurus* and *Meiglyptes tristis*. These species, although more similar to one another than to other species in vertical placement, exhibited numerous differences in their substrate preferences.

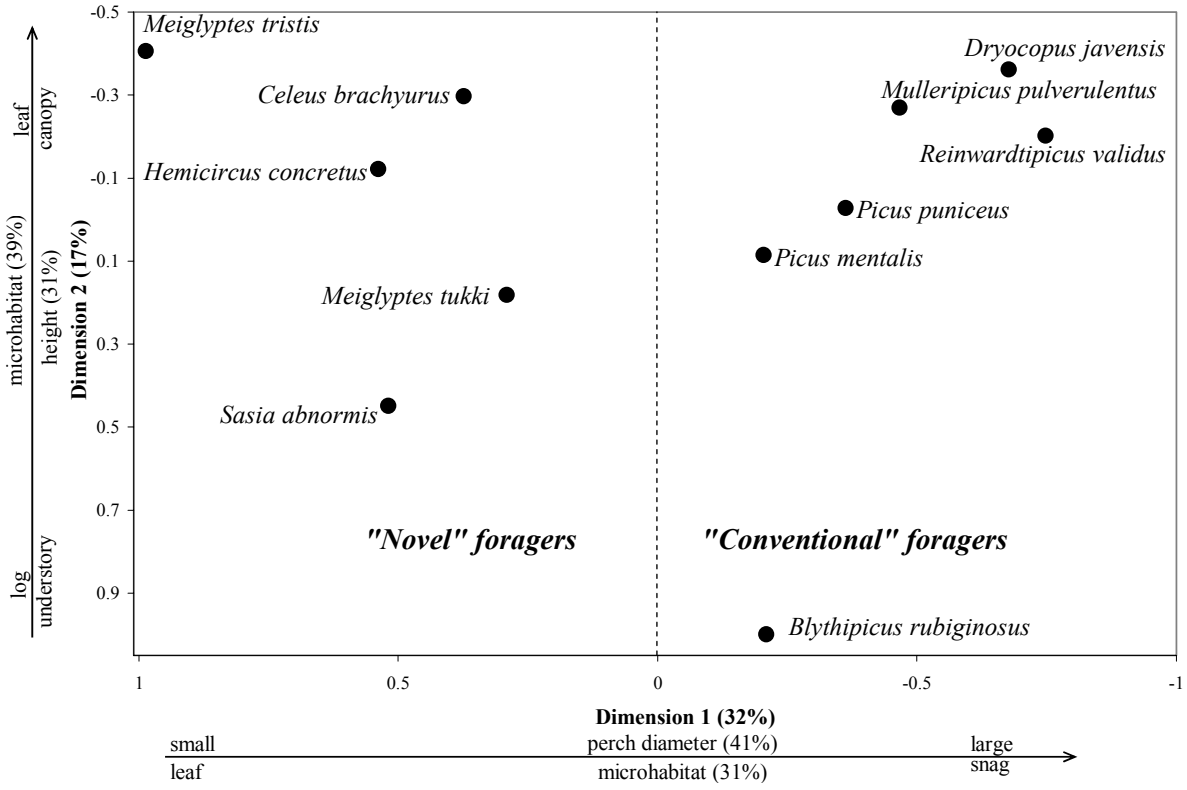


Figure 1.4. Correspondence plot of foraging variables.

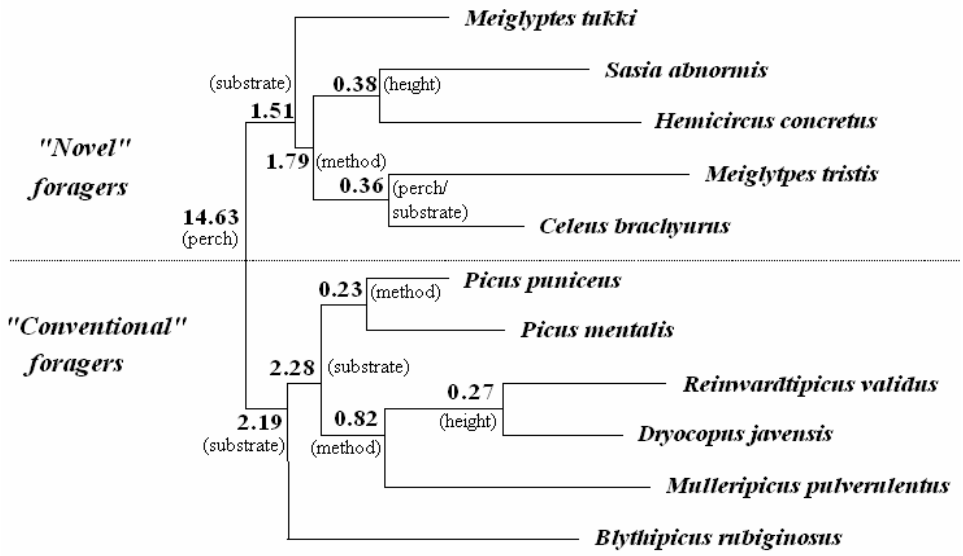


Figure 1.5. Additive ecological tree of foraging variables.

Table 1.4. Additive dissimilarity matrix of 11 woodpecker species (*Dinopium rafflesii* and *Picus miniaceus* not included due to small sample size).

	BR	CB	DJ	HC	MP	MT	MTU	PM	PP	RV	SA
BR	0.00										
CB	0.46	0.00									
DJ	0.51	0.44	0.00								
HC	0.57	0.42	0.51	0.00							
MP	0.51	0.41	0.37	0.52	0.00						
MT	0.57	0.36	0.59	0.43	0.61	0.00					
MTU	0.41	0.38	0.46	0.41	0.47	0.40	0.00				
PM	0.34	0.39	0.47	0.51	0.42	0.49	0.38	0.00			
PP	0.39	0.37	0.34	0.45	0.35	0.53	0.32	0.23	0.00		
RV	0.44	0.56	0.27	0.64	0.45	0.60	0.44	0.35	0.35	0.00	
SA	0.43	0.44	0.47	0.38	0.59	0.50	0.32	0.47	0.42	0.55	0.00

The most ecologically similar species, *Picus mentalis* and *P. puniceus*, differed significantly only for the parameter "Attack Maneuver" (Chi-square = 16.5, df = 5, p = 0.006). *Picus puniceus* excavated whereas *Picus mentali*s more frequently probed into crevices and loose bark more frequently. Other groups of similar species differed significantly in at least three parameters (horizontal placement ($p < 0.0001$), vertical placement ($p < 0.0001$), and perch diameter ($p = 0.001$) for *Sasia abnormis* and *Hemicircus concretus*; horizontal position (p =

0.02), vertical placement ($p = 0.0004$), and attack maneuver ($p = 0.006$) for *Reinwardtipicus validus* and *Dryocopus javensis*; and horizontal position ($p = 0.001$), attack maneuver ($p = 0.02$), perch diameter ($p < 0.0001$), and substrate ($p = 0.0002$) for *Celeus brachyurus* and *Meiglyptes tristis*).

Woodpecker Surveys in Logged and Unlogged Forest

Overall woodpecker abundances differed markedly between PFR and SLFR. This difference could be due to the different sampling protocol between the two sites, most notably the use of different distance estimation techniques (Tables 1.5 and 1.6). Although morning and afternoon transects were conducted at PFR, only morning transects were conducted at SLFR. But there were no apparent differences in morning and afternoon transects in terms of diversity or abundance of woodpeckers.

A likelihood-ratio Chi-square test of transects revealed that overall woodpecker abundance differed only slightly between the two forest types at PFR (40-year-old logged and unlogged). However, binomial tests indicated that individual species differed significantly between the two forest types, with *Meiglyptes tristis, Reinwardtipicus validus*, and *Dryocopus javensis* significantly more abundant in unlogged forest (*Picus puniceus* was more abundant but not significantly so), and *Picus mentalis* significantly more abundant in logged forest (Styring and Ickes 2001).

At SLFR, a likelihood-ratio Chi-square test indicated that overall woodpecker abundance differed significantly among all three forest types (5-year-old logged, 10-year-old logged, and unlogged) binomial tests detected differences in individual species among sites. *Meiglyptes tristis, Blythipicus rubiginosus*, *Celeus brachyurus*, and *Picus miniaceus* were all more abundant in the 5-year-old logged forest than in any other forest type. The rest of the species (with the

exception of *Dinopium rafflesii*, which was rarely seen during transect censuses) were most common in the unlogged forest. Some of these species exhibited a bimodal trend in abundance with species being more common in the 5-year-old and unlogged forest than in the 10-year-old logged forest (*Sasia abnormis, Picus puniceus, Dryocopus javensis, and Mulleripicus pulverulentus*). Other species exhibited a more-expected linear increase in abundance with forest age (*Hemicircus concretus, Meiglyptes tukki, Picus mentalis, and Reinwardtipicus validus*). Interestingly, no species was most abundant in the 10-year-old logged forest.

Table 1.5. Relative abundances and density estimates of woodpeckers in 45 year old logged and unlogged forest at Pasoh Forest Reserve, West Malaysia. Numbers are the total numbers of individuals seen in each forest type during transect surveys. Binomial P = binomial probabilities calculated on species by species and overall abundances. G is the likelihood ratio chi square value calculated across species and between forest types.

SPECIES	ENGLISH NAME	Logged	Unlogged	Binomial p value
Sasia abnormis	Rufous Piculet	0	1	0.50
Hemicircus concretus	Grey-and-Buff Woodpecker	1	*	0.50
Meiglyptes tristis	Buff-rumped Woodpecker	4	14	0.01
Meiglyptes tukki	Buff-necked Woodpecker	4	5	0.25
Celeus brachyurus	Rufous Woodpecker	2	4	0.23
Picus puniceus	Crimson-winged Woodpecker	12	7	0.10
Picus mentalis	Checker-throated Woodpecker	20	1	0.00
Picus miniaceus	Banded Woodpecker	4	2	0.23
Blythipicus rubiginosus	Maroon Woodpecker	1	4	0.16
Dinopium javanense	Common Goldenback	4	*	0.06
Dinopium rafflesii	Olive-backed Woodpecker	0	2	0.25
Reinwardtipicus validus	Orange-backed Woodpecker	6	15	0.03
Dryocopus javensis	White-bellied Woodpecker	1	6	0.05
Mulleripicus pulverulentus	Great Slaty Woodpecker	0	1	0.50
G = 31.6 (df = 5)	**Total**	**59**	**62**	**0.07**
p < 0.001	**Density (individuals/10ha)**	**1.8 +/-1.0**	**2.2 +/-1.3**	

Estimated densities of woodpeckers at PFR and SLFR differed greatly (Tables 1.5 and 1.6). These differences are not too surprising because densities at PFR were based on much more accurate estimates of distance. The higher density estimates from SLFR suggest that the observer (ARS) tended to underestimate the distances of species. However, the calculations from SLFR do establish real differences between the 5-year-old, 10-year-old logged and unlogged sites. The much more open canopy may translate to an ability to detect more species at

longer distances. This analysis clarified differences not readily apparent from the raw data by reducing the apparent difference between 5-year-old and 10-year-old logged forest abundances, and by emphasizing the difference between both logged stands and the unlogged forest.

Table 1.6. Relative abundance and density estimates for woodpeckers at Sungai Lalang Forest Reserve, West Malaysia. The columns L5/10, L10/UL, and UL/L5 are probability values of binomial tests comparing 5 and 10-year-old logged forest (L5/L10), 10-year-old and unlogged forest (L10/UL), and unlogged and 5-year-old logged forest (UL/L5).

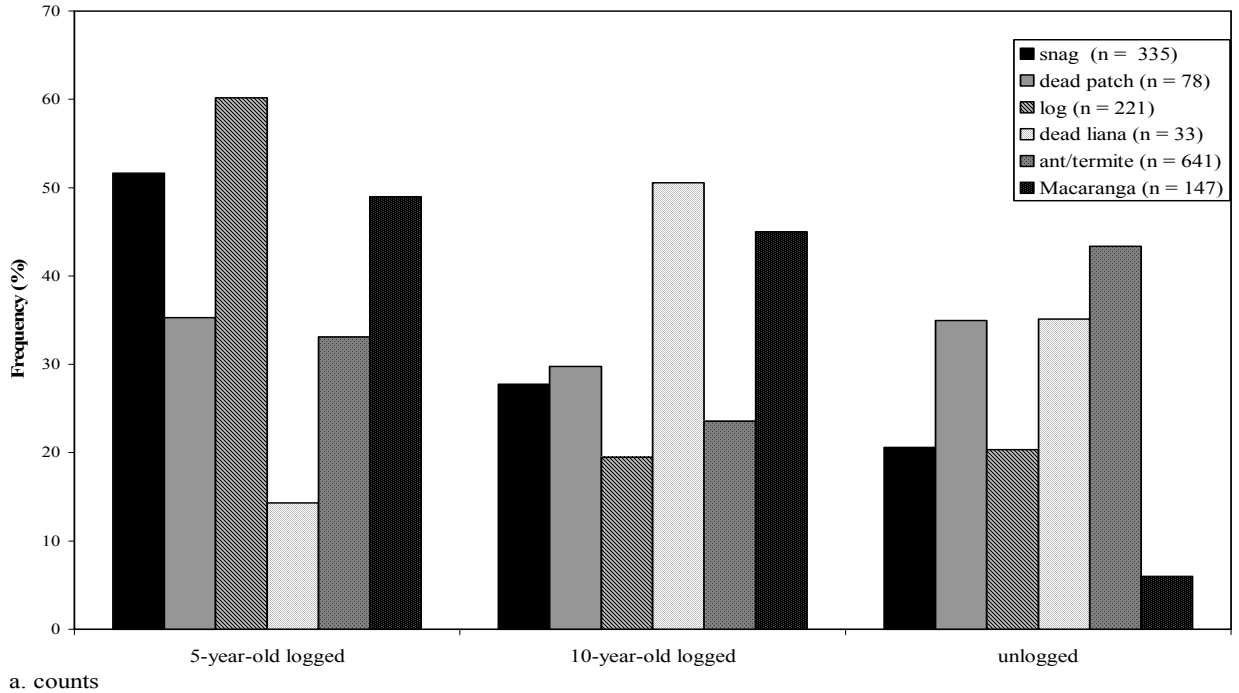
SPECIES	**Logged (5 year)**	**Logged (10 year)**	**Unlogged**	**L5/L10**	**L10/UL**	**UL/L5**
Sasia abnormis	5	1	4	0.09	0.16	0.25
Hemicircus concretus	1	2	9	0.38	0.03	0.01
Meiglyptes tristis	11	5	4	0.07	0.25	0.04
Meiglyptes tukki	3	2	19	0.31	0.00	0.00
Celeus brachyurus	15	*	7	0.00	0.01	0.04
Blythipicus rubiginosus	15	11	8	0.12	0.14	0.06
Picus mentalis	4	12	24	0.03	0.02	0.00
Picus miniaceus	7	0	1	0.01	0.50	0.03
Picus puniceus	11	3	14	0.02	0.01	0.13
Dinopium rafflesii	1	1	*	0.50	0.50	0.50
Reinwardtipicus validus	4	10	14	0.06	0.12	0.01
Dryocopus javensis	12	1	14	0.00	0.00	0.14
Mulleripicus pulverulentus	8	0	5	0.00	0.03	0.16
G = 35.0 (df = 10), p<0.001	**97**	**48**	**123**	**0.00**	**0.00**	**0.01**
Density (indivuals/10 ha)	**4.9+/-2**	**4.5+/-1.9**	**7.8+/-2.9**			

Microhabitat Availability and Use

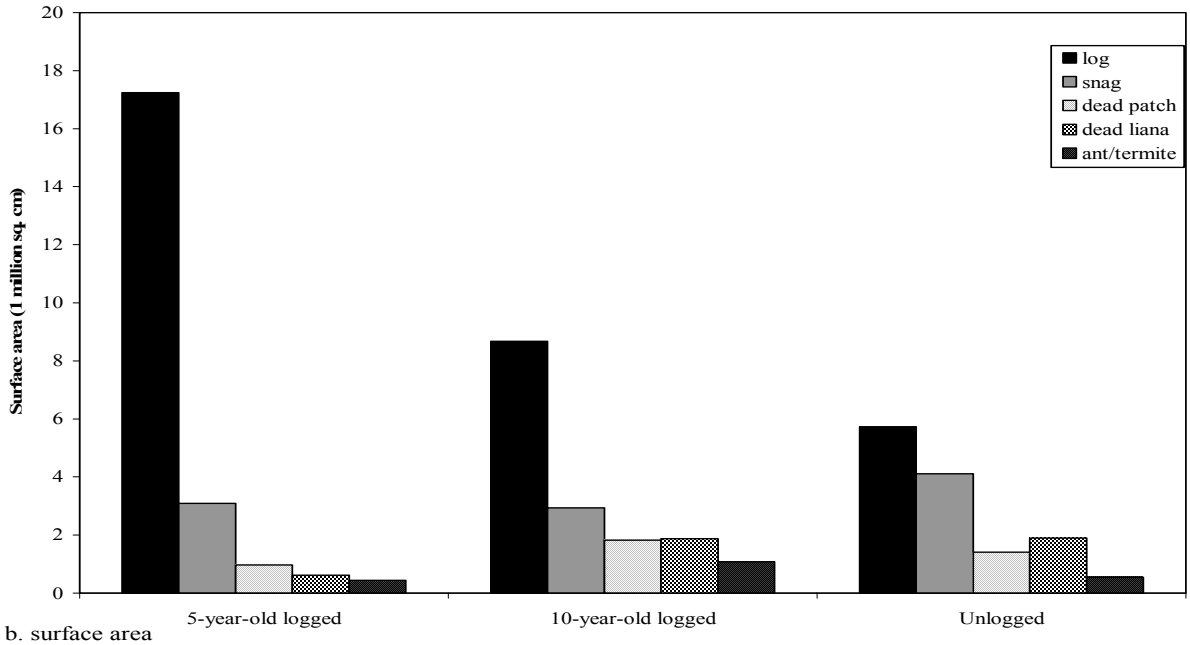
Snags were most abundant in unlogged forest, whereas logs were most abundant in 5-year-old logged forest (Figure 1.6). Dead patches and dead lianas were more abundant in the 10-year-old logged and unlogged forest than in the 5-year-old logged forest, and ant/termite nests were less abundant the 5-year-old and unlogged forest than in the 10-year-old logged forest. *Macaranga* trees were most abundant in 5-year-old logged forest.

When considering resources used at expected or greater than expected rates, many species exhibited fairly clear one-to-one relationships between abundance and availability of certain microhabitats (Figure 1.7.). Other species (such as *B. rubiginosus*) used a variety of

microhabitats and probably used slightly different resources in different forest types (although sample size was too small to determine concrete examples).



a. counts



b. surface area

Figure 1.6 a-b. Abundance of foraging resources in SLFR. (1 ha. sampled at each site). (a) frequencies (b) surface area.

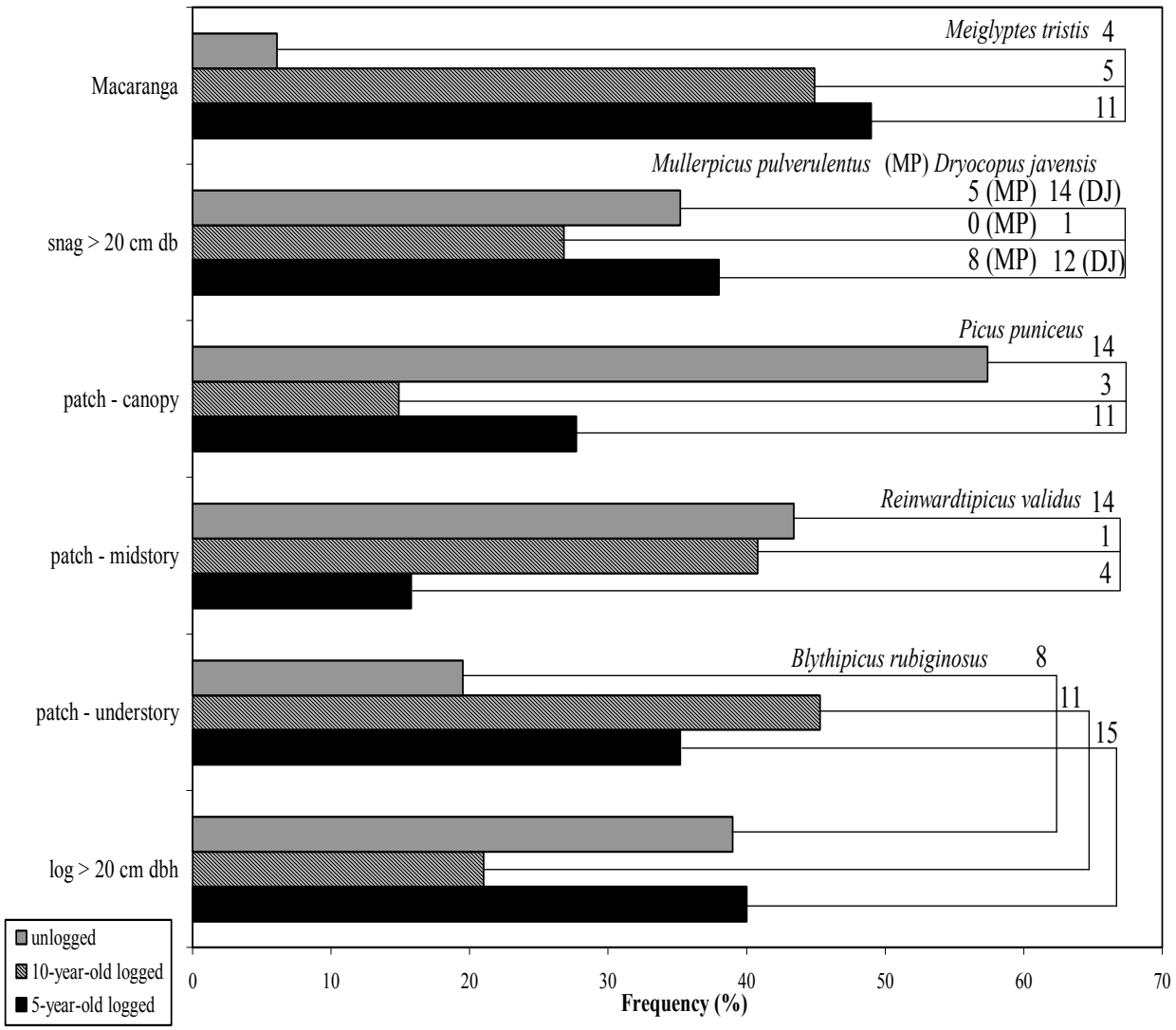
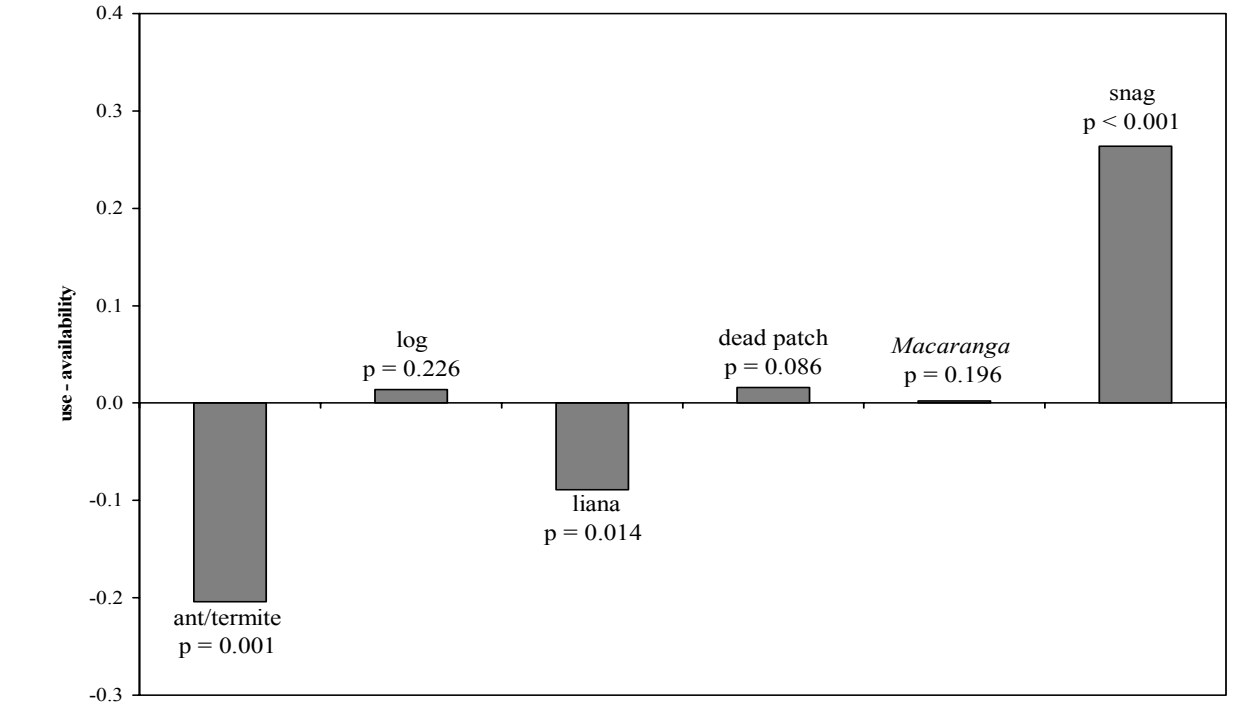
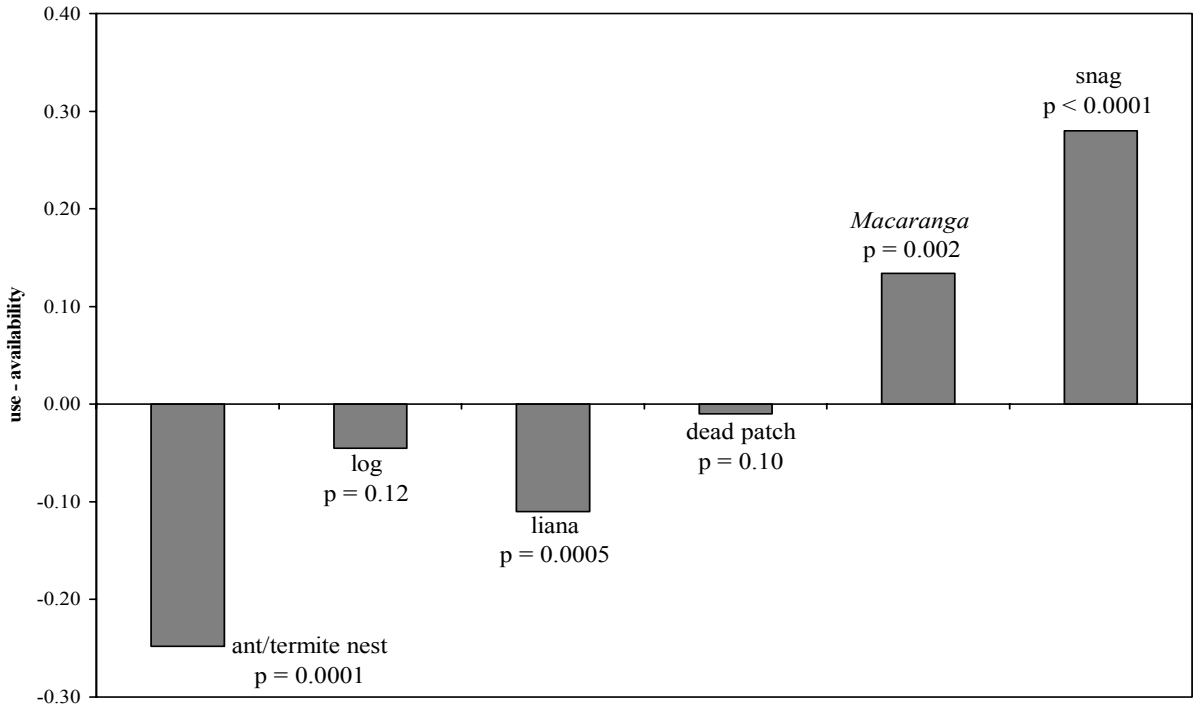


Figure 1.7. Availability of microhabitats (bars) and abundance of selected woodpeckers (numbers) at SLFR.

Binomial tests on use vs. availability values indicated that snags were a strongly preferred substrate in all forest types, whereas ant/termite nests and lianas were less preferred, and Macaranga, dead wood patches, and logs were used in similar proportion to their availability (Figure 1.8 a-d). The strong preference for snags in all forest types supports the suggestion that snags are important in determining the abundance of woodpeckers found in logged forest.

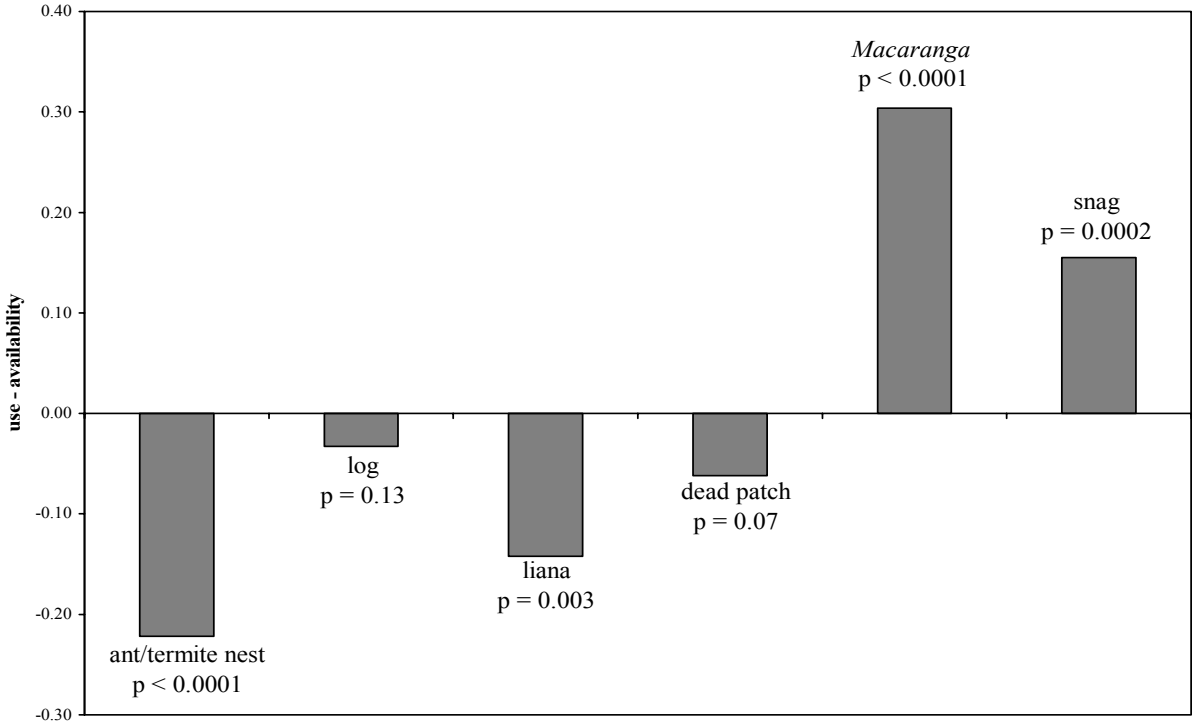


a. all forest types

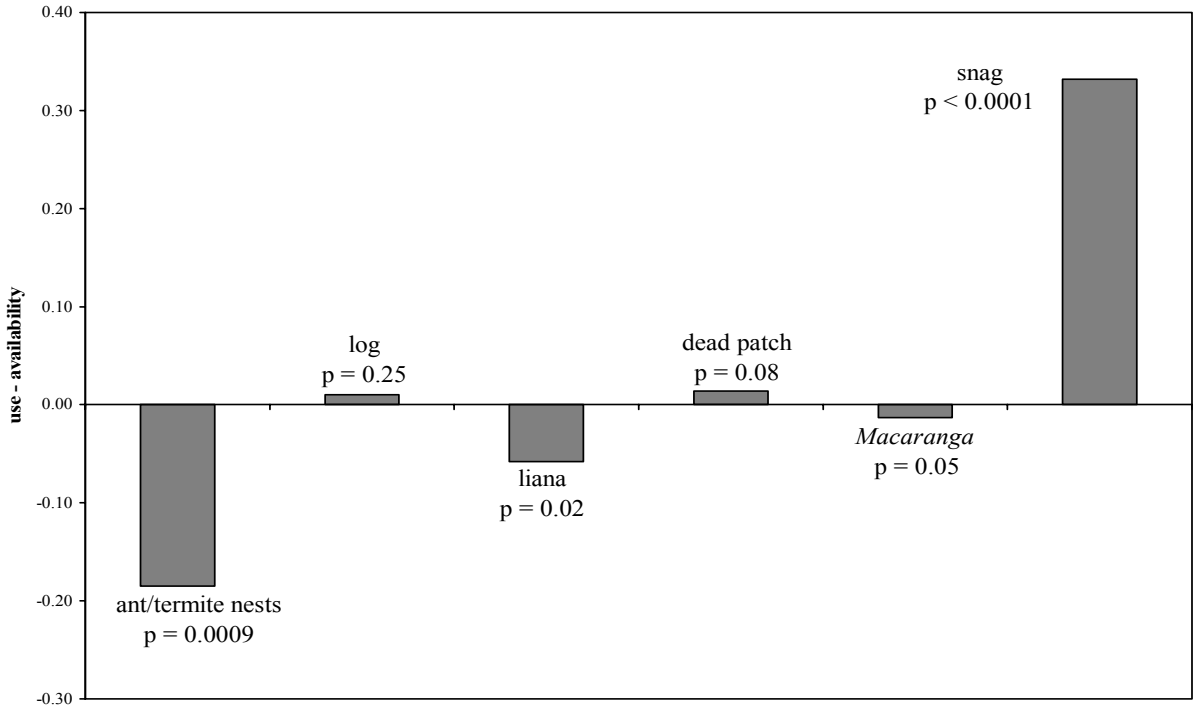


b. 5-year-old logged forest

Figures 1.8 a.-d. Proportional resource use minus proportional resource availability at SLFR. (a) 5, 10, and unlogged forests combined (b) 5-year-old (c) 10-year-old (d) unlogged. (continued)



c. 10-year-old logged forest



d. Unlogged forest

Discussion

Analyses of foraging behavior revealed that the Malaysian woodpeckers exhibited a great range in resource use. They partitioned foraging resources spatially by using different perches (for woodpecker, a perch is frequently also its foraging substrate) and by foraging at different levels in the forest. These birds also exhibited a variety of microhabitat preferences ranging from typical substrate use of live and dead wood of various types to foraging primarily on ant or termite nests, bamboo, and even leaves. The variables 'perch diameter' and 'substrate' in particular were important in dividing this group into two primary subguilds: (1) the larger-bodied woodpeckers that foraged either on dead wood patches (*Blythipicus rubiginosus, Picus puniceus,* and *P. mentalis*), or on snags (*Reinwardtipicus validus, Dryocopus javensis,* and *Mulleripicus pulverulentus*), and (2) the smaller-bodied woodpeckers that foraged more on substrates seldom used by temperate latitude woodpeckers, such as bamboo (*Sasia abnormis* and *Hemicircus concretus* to a lesser extent), ant nests (*Meiglyptes tristis, M. tukki,* and *Celeus brachyurus*), leaves (*Meiglyptes tristis)*, and *Macaranga* trees (*Meiglyptes tristis* and *Celeus brachyurus* to a lesser extent).

Of the subguild of birds that foraged on 'novel' substrates, *Meiglyptes tristis* displayed unique foraging preferences. This species foraged primarily on leaves, quite often on pioneer trees in logged forest, small trees in large treefall gaps, and even on bamboo leaves. However, *M. tristis* strongly preferred the leaves of *Macaranga* trees. Tree species in the genus *Macaranga* are prevalent pioneer species in Malaysian forests, and they are known to have mutualistic associations with ants in the genus *Crematogaster*. The large leaves of *Macaranga* are found at the tip of each branch. Petioles extend from these flaky tips, and *M. tristis* foraged frequently on both the leaves and flaky tips. ARS disturbed these tips on numerous occasions, and inevitably,

small ants would run out. Tiny ant nests were also found at the base of bamboo leaves. It is possible that *M. tristis* was eating ants while foraging on leaves. When not foraging on leaves, this species foraged on ant and termite tunnels on tree branches and also on ball-shaped ant nests suspended in trees.

In this study, significant changes in the woodpecker community associated with logging were documented. Because the census results from the two sites were different, we put things in context by comparing these results with other studies (Table 1.7).

At PFR, only a few species were common enough to make any conclusion based on my results, so we will discuss primarily results from SLFR and mention those common species from PFR in context. At SLFR three patterns of abundance prevailed: (1) some species were most common in the 5-year-old logged forest and least common in the unlogged forest, (2) some species were most common in the unlogged forest and least common in the 5-year-old logged forest, and (3) some species were much more common in the unlogged forest and the logged forest than in the 10-year-old forest. No species was most common in the 10-year-old forest.

The species that followed pattern one (most common in 5-year-old logged forest and least common in unlogged forest) were *Meiglyptes tristis, Celeus brachyurus, Picus miniaceus,* and *Blythipicus rubiginosus*. The first two *M. tristis*, *C. brachyurus*, and probably *P. miniaceus* (although sample size is lacking for this species) foraged primarily on ants and termites, although they obtained them from different substrates (*Macaranga* for *M. tristis* and ant/termite tunnels and nests in trees for *C. brachyurus*). *Blythipicus rubiginosus* foraged on dead wood, but was restricted to the understory, where wood was more prevalent in the logged forests in the form of stumps and logs. Unlike at SLFR, where *M. tristis* was more common in the logged forest, this species was more common in unlogged forest at PFR. The managed forest at PFR was logged

more than 40 years ago, however, and over time the stand architecture must have changed considerably. Stand structure in the selectively logged forest at PFR during the time of this study was typical of older, managed forests in which lianas and rattans have also been removed: uniformly aged with relatively few snags and climbers and thus few large gaps. *Meiglyptes tristis* occurs frequently in primary forest (Styring and Ickes 2001) with associated large treefall and canopy gaps and young secondary forests with higher light levels and dense vegetation closer to the ground. Conversely, *M. tristis* is much less common in older logged forests (Styring and Ickes 2001) and tree plantations (Mitra and Sheldon 1993), where the vegetation is more uniform and gaps are less common.

The following species followed pattern two (most common in unlogged forest and least common in 5-year-old logged forest): *Hemicircus concretus, Meiglyptes tukki, Picus mentalis,* and *Reinwardtipicus validus*. Because *H. concretus* foraged on branches and branchlets (mostly live) in the canopy, ARS was unable to sample adequately their primary substrate. This species may prefer to forage high in the canopy, and therefore avoids the low stature, recently logged forest. *M. tukki* foraged on ant/termite nests in the understory, and these showed a linear increase from recently logged to unlogged forest. Although the sample size was small from PFR, there was little difference in *M. tukki* abundance at the unlogged and logged sites at PFR, so this bird may do well in logged, regenerating forest. *Picus mentalis* foraged primarily on fairly large dead wood patches in the midstory. The same management techniques that might have caused *M. tristis* to be less abundant in older logged forest may be beneficial to *P. mentalis*. M. Lammertink (unpubl. data) suggested that *P. mentalis* abundance is negatively correlated with the presence of understory vegetation and may explain why it does better in old logged

forest at PFR. The same explanation may be true for *R. validus,* which also preferred to forage in the understory and midstory.

Finally, the following species followed pattern three (more common in unlogged forest and 5-year-old logged forest than in 10-year-old logged forest): *Sasia abnormis, Picus puniceus, Dryocopus javensis,* and *Mulleripicus pulverulentus*. *Sasia abnormis*, the smallest species in this system, foraged frequently on small lianas and branchlets of trees and bamboo in the lower levels of the forest. The absence of this microhabitat in older logged forest (due to an open, homogeneous understory) may explain the low abundance *S. abnormis* in that habitat. In logged forest, it foraged on bamboo (as well as rattan and sometimes the petioles of suspended *Macaranga* leaves), but in unlogged forest, it used lianas found in treefall gaps. The other three species foraged on dead wood (patches for *P. puniceus* and snags for *D. javensis* and *M. pulverulentus* – the largest woodpeckers in the system). The absence of large trees and snags in older logged forest is the limiting factor here.

Table 1.7. Summary data on the effects of logging on woodpeckers in Southeast Asian rainforests. Numbers represent raw abundances (data taken only from studies that presented raw abundances). Numbers in parenthesis are percentages of the total abundance.

Author	Location	Primary	Logged (1-9 yr.)	Logged (10-12 yr.)	Logged (25+ yr.)
Johns (1995)	Ulu Segama FR, Sabah	30 (43)	23 (33)	15 (23)	-
Styring (this paper)	Sungai Lalang FR, W. Malaysia	123 (47)	97 (36)	48 (18)	-
Hasan & Hussin (1997)	Ulu Segama FR, Sabah	64 (54)	55 (46)	-	-
Lambert (1992)	Ulu Segama FR, Sabah	35 (83)	-	7 (17)	-
Wong (1985)	Pasoh FR, W. Malaysia	28 (51)	-	-	27 (49)
Styring & Ickes (2001)	Pasoh FR, W. Malaysia	62 (51)	-	-	59 (49)
Average		**57 (31)**	**58 (32)**	**24 (13)**	**43 (24)**

Although woodpeckers were able to use novel resources that were available in the logged forest, the substrates that were frequently used by woodpeckers (dead wood patches and snags) were abundant in the unlogged forest. Both logged sites had lower abundance of resources than the unlogged forest, and the main difference between the five and 10-year-old logged forest was the abundance of dead wood. Because of the damage caused by tree felling and extraction, the five-year-old site had a relatively high abundance of logs and snags. As this residual dead wood decayed, few new snags or treefalls occurred, and the older logged stand was depauperate in these important resources. This evidence of a time lag in the impacts of logging for woodpeckers is supported by other studies (Johns 1989, 1992, Styring and Ickes 2001). Other resources such as dead wood patches were more abundant in the 10-year-old logged stand, but these resources were less important than snags in determining the abundance of a majority of species.

Management Implications/Research Suggestions

Logging and extraction practices varied widely among PFR and SLFR and even between the two sites at SLFR. However, a superficial look at the results would suggest that limited logging is not particularly harmful to woodpeckers. However, density estimates indicated a dramatic difference between younger (<10 years) logged forest and unlogged forest. Although this study involved a low sample of study sites (n = 3 for SLFR, and n = 2 for PFR), numerous other studies suggest that there is a time lag in the effects of logging on woodpeckers in Malaysian rainforests. Woodpecker abundances appear to drop dramatically approximately 10 years after logging, and, although numbers recover over time, community structure can remain altered for at least 45 years into the stand cycle (Table 1.7).

In temperate forests, management effects on woodpeckers are intensely studied, and in some areas, management guidelines are almost exclusively aimed at maintaining woodpecker (particularly large-bodied woodpeckers) and secondary-cavity-nester populations. Much of the focus has been on management of nesting habitat for large woodpeckers (Flemming et al. 1999). However, other studies indicate that understanding the foraging ecology of woodpeckers is an essential prelude to effective forest management (Conner et al. 1994, Welsh and Capen 1992). The preliminary results of this study suggest that many findings for temperate woodpeckers (maintaining mature and dead trees in logged stands) also apply in the tropics. In fact, tree retention may be even more important in the tropics, where decay rates are rapid and snags are likely less abundant than in temperate forests (Gibbs et al. 1993, Pattanavibool and Edge 1996). Numerous secondary-cavity-nesters, such as hornbills, owls, and several mammal species, presumably would benefit from such management practices as well.

CHAPTER 3
PATTERNS OF ECOLOGICAL AND MORPHOLOGICAL DIVERSITY IN WOODPECKER ASSEMBLAGES

Introduction

Understanding patterns of biological diversity is a multifaceted pursuit that involves complex interactions between historical and ecological factors. Such investigations often require making comparisons across a range of habitats and regions. Comparing data sets across such large spatial scales can be difficult because the ecological variables collected in these data sets are often contingent on environmental factors that vary across spatial gradients (Ricklefs and Miles 1994). To minimize this problem, morphology is often used as a surrogate for ecology. One advantage of using morphological data is their relative ease of interpretation and repeatability of measurements (Ricklefs and Miles 1994).

Woodpeckers are good model organisms for an investigation of large-scale patterns of diversity for a number of reasons. They are widespread and found on every major landmass except Antarctica and Australia (Figure 2.1). They also exhibit relatively similar patterns of diversity across environmental, elevational, and latitudinal gradients as other taxa. Although woodpeckers can be found in some treeless habitats such as savannas and high montane areas, they are more diverse in forested habitats, and their highest diversity occurring in tropical rainforests (Figure 2.2, Table 2.1).

Woodpeckers are also well suited to ecomorphological studies because of their highly derived morphology and specialized ecology. In all of their habitats, woodpeckers not only form a distinct taxonomic group, but also a relatively discrete ecological guild. Their foot, tail, and especially skull morphology is adapted for excavating hard substrates (usually wood) for food and nesting space (Bock 1959, 1964, 1966).

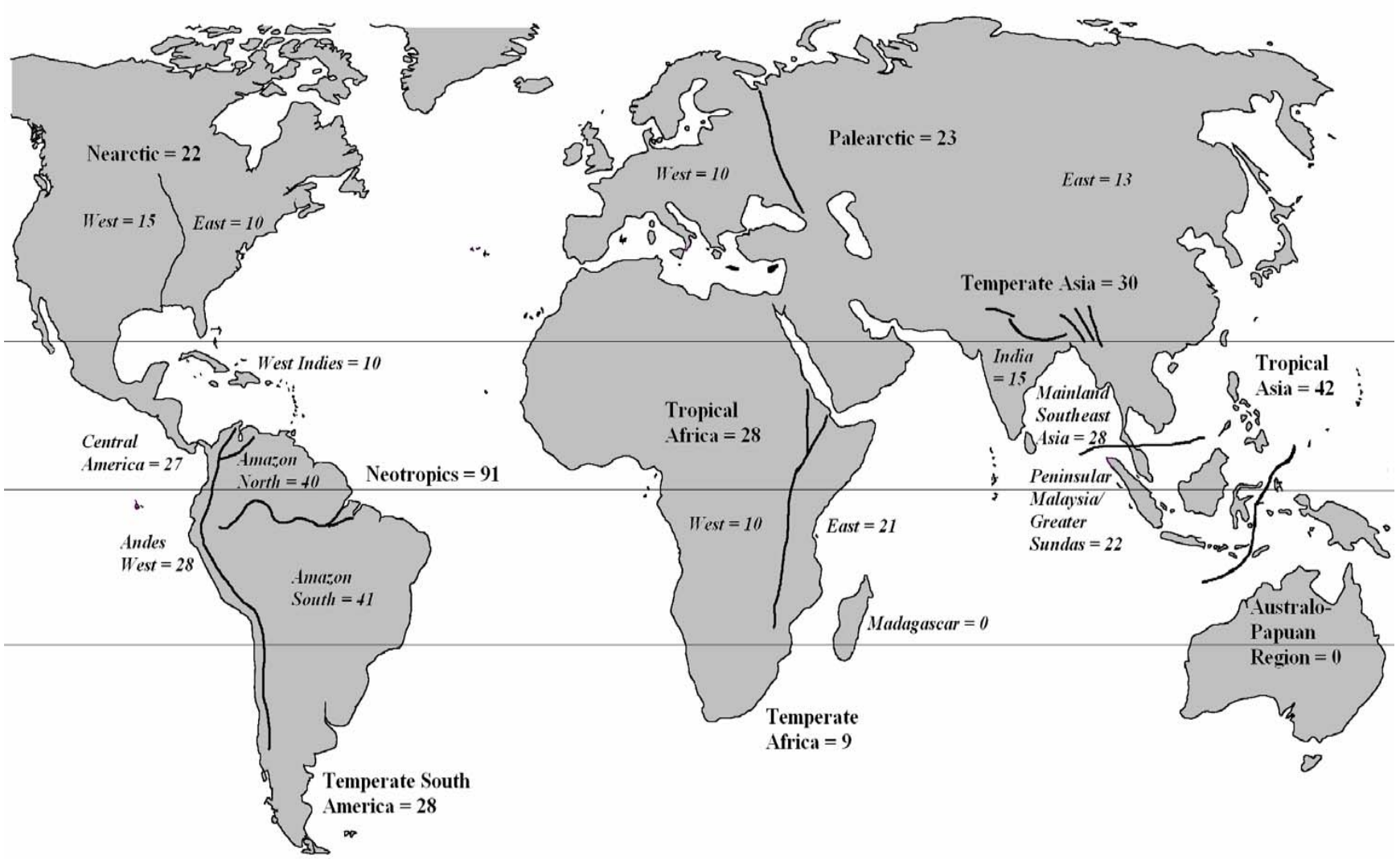


Figure 2.1. Distribution of the 214 species of woodpeckers.

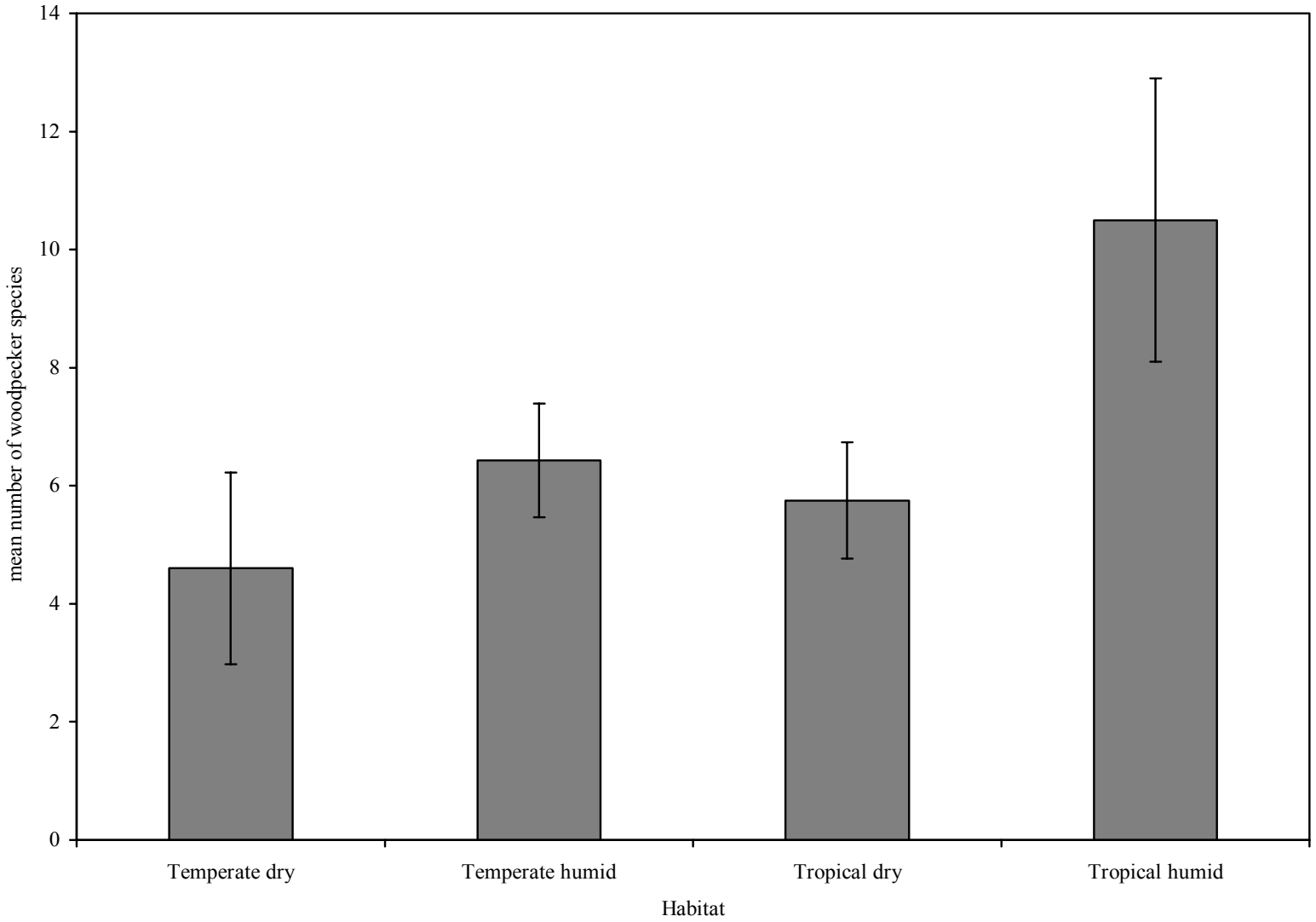


Figure 2.2. Comparison of woodpecker species richness in temperate and tropical forests. For a list of sites, see Table 1.

Table 2.1. Species richness for woodpeckers at 34 sites.

Type	Location	Number	Citation
	Texas	7	Peterson 1998
Temperate	Utah	6	Wauer 1965
Dry/Open	South Africa	3	Short 1971
(Mean = 5.4)	India	3	Sankar et al. 1993
	India	4	Pandav 1996
	Louisiana	6	Ingold 1995
	Minnesota	7	Askins 1983
Temperate	Nova Scotia	7	Tufts 1917
Humid/Closed	Northwest Territories	7	Scotter et al. 1985
(Mean = 6.4)	Slovakia	8	Kristin in press
	China (Liaoning)	4	Brazil 1992
	China (Sichuan)	6	King 1989
	Brazil	6	Tubelis and Cavalcanti 2001
	Brazil	7	Silveira 2000
Tropical	Bolivia	6	Kratter et al. 1993
Dry/Open	Tanzania	5	Selempo 1993
(Mean = 5.8)	Zambia	6	Britton 1970
	Kenya	4	Wilson 1994
	Burma	8	Robson et al. 1998
	Cambodia	4	Duckworth and Hedges 1997
	Guatemala	7	Askins 1983
	Panama	8	Karr et al. 1990
	Venezuela	13	Zimmer et al 1997
Tropical	Brazil	12	Parker and Goerck 1997
Humid/Closed	Brazil	13	Stotz et al. 1997
(Mean = 10.5)	Peru	16	Karr et al. 1990
	Ivory Coast	5	Thiollay 1985
	Liberia	5	Kofron and Chapman 1995
	Gabon	7	Thiollay 1985
	Uganda	3	Owiunji and Plumptre 1998
	Laos	16	Duckworth et al. 1998
	Vietnam	14	Robson et al. 1993
	Malaysia	13	Johns 1989
	Malaysia (Borneo)	15	Lambert 1992

Methods

Ecological Data

Ecological data were collected from five sites: two sites in West Malaysia and one site each in Guatemala, Maryland, and Minnesota. The two sites in Malaysia (Pasoh Forest Reserve, and Sungai Lalang Forest Reserve) are both classified as lowland dipterocarp rainforest, and

observations (n > 500) were made by the author for 12 months from 1998 to 2000 (for details, see Chapter 1). Observations from the remaining three sites (n > 900) were made by Robert A. Askins from 1977 to 1979 (Askins 1983). The forest at the Guatemala site (Tikal National Park) was considered intermediate between tropical dry forest and low subtropical moist forest. The sites in Maryland (Chesapeake Bay Center for Environmental Studies) and Minnesota (Chain of Lakes Park) were both considered temperate deciduous, but species composition and structural aspects of each forest differed (see Askins 1983).

Six microhabitat variables, three foraging maneuvers, and five perch diameter classes (Table 2.2 and 2.3) were analyzed by using Correspondence Analysis (CA). Because microhabitat and foraging maneuver are not entirely independent from one another, these variables were combined for the analysis (see Miles and Rickleffs 1984). Two separate analyses were performed: one including perch classes, and one without. The object of these analyses was to determine ecological relationships among species and define foraging space for correlation with morphological data. Analyses were run by using the CORRESP procedure in SAS 8.00 (1999).

Morphological Data

Morphometric dimensions were measured from museum specimens taken for each species included in the ecological analyses. Specimens were selected from localities as close as possible to the areas where field observation were made. A minimum of five male specimens was measured per species (10 measurements per specimen; Table 2.4). Measurements were log-transformed to reduce skewness in the data and homogenize variances. Because the species in this data set vary in size by several orders of magnitude (*Sasia abnormis* mean mass = 9 g, and *Mulleripicus pulverulentus* mean mass = 430 g; Short 1978), a separate data set reflecting shape

Table 2.2. Foraging data for woodpeckers from sites in Malaysia, Guatemala, Maryland, and Minnesota. MD = Maryland, MN = Minnesota.

		Perch diameter					Microhabitat						Maneuver		
English Name	**Species**	**XS**	**S**	**M**	**L**	**XL**	**LW**	**DW**	**AT**	**FT**	**LF**	**Brm**	**EX**	**GL**	**PR**
Rufous Piculet	*Sasia abnormis*	0.70	0.30	0.00	0.00	0.00	0.73	0.20	0.03	0.00	0.05	0.00	0.83	0.18	0.00
Grey and Buff Woodpecker	*Hemicircus concretus*	0.26	0.69	0.03	0.03	0.00	0.64	0.31	0.00	0.00	0.03	0.03	0.56	0.36	0.08
Buff-rumped Woodpecker	*Meiglyptes tristis*	0.28	0.58	0.10	0.00	0.04	0.61	0.10	0.16	0.00	0.14	0.00	0.41	0.34	0.26
Buff-necked Woodpecker	*Meiglyptes tukki*	0.32	0.42	0.13	0.10	0.03	0.33	0.23	0.43	0.00	0.00	0.00	0.77	0.23	0.00
Rufous Woodpecker	*Celeus brachyurus*	0.05	0.32	0.55	0.00	0.09	0.52	0.29	0.19	0.00	0.00	0.00	0.52	0.48	0.00
Maroon Woodpecker	*Blythipicus rubiginosus*	0.00	0.29	0.47	0.06	0.18	0.25	0.75	0.00	0.00	0.00	0.00	0.62	0.00	0.38
Checker-throated Woodpecker	*Picus mentalis*	0.02	0.14	0.43	0.18	0.24	0.36	0.60	0.04	0.02	0.00	0.00	0.42	0.19	0.38
Crimson-winged Woodpecker	*Picus puniceus*	0.00	0.09	0.38	0.41	0.12	0.34	0.66	0.00	0.00	0.00	0.00	0.82	0.08	0.11
Orange-backed Woodpecker	*Reinwardtipicus validus*	0.00	0.06	0.12	0.33	0.49	0.06	0.94	0.00	0.02	0.00	0.00	0.96	0.00	0.02
White-bellied Woodpecker	*Dryocopus javensis*	0.00	0.00	0.03	0.36	0.61	0.06	0.95	0.00	0.00	0.00	0.00	0.95	0.03	0.03
Great Slaty Woodpecker	*Mulleripicus pulverulentus*	0.00	0.00	0.45	0.03	0.52	0.35	0.66	0.00	0.00	0.00	0.00	0.86	0.00	0.14
Pale-billed Woodpecker	*Campephilus guatemalensis*	0.00	0.22	0.30	0.28	0.20	0.11	0.89	0.00	0.00	0.00	0.00	0.95	0.00	0.05
Chestnut-colored Woodpecker	*Celeus castaneus*	0.04	0.70	0.09	0.17	0.00	0.35	0.65	0.00	0.00	0.00	0.00	0.87	0.00	0.13
Lineated Woodpecker	*Dryocopus lineatus*	0.00	0.34	0.30	0.25	0.12	0.33	0.67	0.00	0.01	0.00	0.00	0.62	0.00	0.38
Golden-fronted Woodpecker	*Melanerpes aurifrons*	0.10	0.53	0.20	0.13	0.04	0.48	0.52	0.00	0.17	0.00	0.00	0.29	0.00	0.54
Black-cheeked Woodpecker	*Melanerpes pucherani*	0.20	0.47	0.23	0.07	0.03	0.44	0.52	0.00	0.20	0.00	0.03	0.26	0.01	0.53
Golden-olive Woodpecker	*Piculus rubiginosus*	0.44	0.39	0.15	0.01	0.00	0.32	0.61	0.00	0.00	0.00	0.07	0.49	0.00	0.51
Smokey-brown Woodpecker	*Veniliornis fumigatus*	0.20	0.72	0.08	0.00	0.00	0.19	0.81	0.00	0.00	0.00	0.00	0.95	0.00	0.05
Pileated Woodpecker (MD)	*Dryocopus pileatus*	0.08	0.08	0.36	0.31	0.18	0.36	0.64	0.00	0.18	0.00	0.00	0.67	0.00	0.15
Hairy Woodpecker (MD)	*Picoides villosus*	0.09	0.31	0.52	0.07	0.00	0.23	0.77	0.00	0.06	0.00	0.00	0.91	0.00	0.04
Downy Woodpecker (MD)	*Picoides pubescens*	0.33	0.41	0.12	0.13	0.02	0.39	0.61	0.00	0.10	0.00	0.00	0.69	0.00	0.21
Pileated Woodpecker (MN)	*Dryocopus pileatus*	0.00	0.09	0.15	0.45	0.30	0.24	0.76	0.00	0.09	0.00	0.00	0.82	0.00	0.09
Hairy Woodpecker (MN)	*Picoides villosus*	0.04	0.43	0.44	0.07	0.02	0.24	0.76	0.00	0.00	0.00	0.00	0.94	0.00	0.05
Downy Woodpecker (MN)	*Picoides pubescens*	0.43	0.35	0.17	0.04	0.00	0.38	0.62	0.00	0.02	0.00	0.00	0.84	0.00	0.14

Table 2.3. Definitions of the foraging codes used in the analysis.

Parameter	Variable	Definition
Perch diameter	**XS**	Perch is smaller than **5 cm** diameter
	S	Perch is **5-10 cm** diameter
	M	Perch is greater than **10 cm** and less than **25 cm** diameter
	L	Perch is **25 cm** to less than **35 cm** diameter
	XL	Perch is greater **35 cm** diameter or greater
Microhabitat	**LW**	Live wood
	DW	Dead wood
	AT	Ant or termite nest (or run)
	LF	Leaf
	Brm	Bromeliad (epiphyte)
Foraging Maneuver	**EX**	Excavate
	GL	Glean
	PR	Probe
	FT	Fruit eating

was created by regressing each log-transformed measurement against log body length. The two data sets were analyzed independently with Principal Components Analysis in SYSTAT (SPSS Inc. 1998), to determine structure in the morphological data and to produce independent variables.

Correlating Ecological and Morphological Data

Canonical Correlation Analysis (CCA) was used to determine correlation between the ecological and morphological data sets. CCA ordinates data sets to maximize correlation between ecological and morphological variables (Miles and Rickleffs 1984). The first three dimensions of the two Correspondence Analyses (with and without perch classes) were analyzed separately with the log-transformed variables and then again with the regressed variables (for a total of four separate analyses). Factor scores from Principal Components Analysis can also be used in CCA, but direct interpretation is more readily made with the original variables. Data were entered into SAS, and the CANCORR procedure used. As part of CCA, Canonical

Redundancy Analysis (CRA) examined the portion of the variation in the ecological data that explains morphological variation and vice versa.

Ecomorph Classification

Once relationships between ecology and morphology were established with CCA, patterns in morphology in additional woodpecker assemblages were investigated with Discriminate Function Analysis (DFA). DFA is a multivariate classification technique that maximizes differences between specified groups. Two classes ("Conventional" and "Novel") were assigned to species based on microhabitat preference. The following species were classified as "conventional" based on their preference for wood (live wood, snags, dead limbs, knots, etc.): *Blythipicus rubiginosus, Picus puniceus, Picus mentalis, Reinwardtipicus validus, Dryocopus javensis,* and *Mulleripicus pulverulentus* (Malaysia), and *Dryocopus pileatus, Picoides villosus*, and *Picoides pubescens* (Maryland and Minnesota). The following species (all from Malaysia) were classified as "novel" based on their preference for 'novel' microhabitats such as bamboo and leaves (see Chapter 1): *Sasia abnormis, Hemicircus concretus, Meiglyptes tristis, Meiglyptes tukki*, and *Celeus brachyurus*.

Once a classification based on known foraging ecology was established and the relationship between ecology and morphology established, species were classified from other tropical and temperate sites where the foraging ecology has not been studied in detail based on their morphology. Assemblages from the following regions were analyzed: Minnesota (seven species), Europe (six species; Kristin in press), temperate China (six species; King 1989), Gabon (six species; Thiollay 1988), and Peru (12 species; Karr et al. 1990). For each of these 47 species, five male specimens were measured (10 measurements per specimen; Table 2.5). These measurements were then entered into DFA without a classification, and DFA assigned

Table 2.4. Mean morphometric measurements for 21 woodpecker species at sites in Malaysia, Guatemala, Maryland (MD), and Minnesota (MN).

Species	Wing	Tail	Body	Culmen	Bill Height	Bill Width	Tarsus	Toe 2	Width - Toe nail 2	Height - Toe nail 2
Sasia abnormis	52.8	25.2	44.7	12.9	5.3	6.0	11.8	7.9	3.5	2.1
Hemicircus concretus	82.5	38.8	78.0	20.2	7.0	7.9	16.8	11.7	5.0	3.6
Meiglyptes tristis	94.4	56.9	88.4	19.3	6.9	8.1	18.6	11.4	5.1	3.6
Meiglyptes tukki	99.9	72.8	94.8	24.2	8.3	10.4	20.3	12.4	7.5	4.6
Celeus brachyurus	111.3	67.8	111.2	22.6	8.2	9.3	23.4	12.4	6.8	4.5
Blythipicus rubiginosus	120.0	78.0	112.4	34.5	9.5	11.4	27.7	15.0	8.9	5.6
Picus mentalis	131.6	103.2	133.2	33.5	10.6	11.7	27.5	15.0	9.3	6.2
Picus puniceus	129.7	98.7	123.7	29.3	8.9	9.8	26.9	13.6	8.9	5.7
Reinwardtipicus validus	154.5	104.4	144.7	43.5	12.2	13.8	35.7	15.5	10.4	6.8
Dryocopus javensis	227.5	181.8	225.6	56.6	14.3	17.2	42.5	21.7	13.9	8.8
Mulleripicus pulverulentus	235.7	178.9	255.1	61.8	16.4	16.2	43.5	25.1	15.3	10.5
Campephilus guatemalensis	189.3	131.4	173.8	46.6	12.7	16.2	37.4	18.8	13.0	8.5
Celeus castaneus	123.9	97.6	122.7	24.7	8.1	10.8	27.6	14.7	8.3	5.5
Dryocopus lineatus	171.8	133.2	160.8	37.1	10.8	13.2	32.1	15.7	10.7	7.1
Melanerpes aurifrons	126.2	85.5	115.2	29.7	9.2	10.6	26.6	14.6	7.6	4.9
Melanerpes pucherani	109.1	66.3	94.5	27.0	7.2	8.8	23.1	12.3	6.4	4.3
Piculus rubiginosus	122.5	86.7	114.7	26.4	7.8	10.2	25.6	14.1	7.5	5.2
Veniliornis fumigatus	86.2	65.5	83.3	20.8	6.6	8.4	20.3	9.0	6.0	3.9
Dryocopus pileatus (MD)	230.7	185.7	214.4	50.4	13.2	14.3	39.2	18.8	13.1	8.7
Picoides villosus (MD)	119.5	91.3	110.3	30.4	7.8	9.2	25.2	11.1	7.9	4.9
Picoides pubescens (MD)	90.3	68.3	80.2	16.8	5.2	6.4	18.5	7.7	5.5	3.4
Dryocopus pileatus (MN)	234.7	188.0	224.8	53.8	13.4	15.5	40.3	19.3	13.0	8.8
Picoides villosus (MN)	123.2	95.6	114.2	31.2	8.3	9.7	25.7	11.1	7.8	5.0
Picoides pubescens (MN)	92.2	68.6	76.0	16.5	5.8	6.6	18.6	8.4	5.1	3.3

Table 2.5. Mean morphometric measurements for woodpeckers at sites in Malaysia, Minnesota, Europe, China, Gabon, and Peru.

Species	Origin	Wing	Tail	Body	Cul	BH	BW	Tars	T2	W TN2	H TN2
Picus miniaceus	Malaysia	124.3	91.1	125.7	26.3	9.3	12.3	27.2	14.5	8.3	5.3
Dinopium rafflesii	Malaysia	136.0	117.0	126.6	33.5	10.2	11.5	27.3	12.3	8.9	5.8
Melanerpes erythrocephalus	Minn.	138.4	92.2	115.4	26.9	8.0	10.6	27.1	13.3	7.1	4.5
Sphyrapicus varius	Minn.	123.1	89.8	97.6	23.4	7.1	9.3	23.4	17.1	6.3	4.2
Colaptes auratus	Minn.	152.6	107.3	156.8	34.1	8.4	10.5	30.9	15.8	7.9	5.0
Picoides major	Europe	133.9	102.8	122.4	26.9	8.7	10.3	27.4	11.3	7.8	14.0
Picoides leucotos	Europe	141.3	107.6	133.2	36.7	9.6	12.6	30.7	14.1	9.4	6.0
Picoides medius	Europe	119.9	92.2	117.9	23.1	6.8	8.9	23.9	13.6	8.2	4.9
Picoides minor	Europe	86.2	61.6	75.7	15.2	5.2	6.9	17.4	7.6	5.4	3.3
Dryocopus martius	Europe	235.4	184.9	228.5	58.2	14.7	17.6	44.9	18.8	13.9	8.8
Picus canus	Europe	139.5	119.7	147.8	35.2	8.8	10.7	30.8	14.9	9.7	6.2
Picoides hypertherius	China	119.9	91.1	96.8	24.3	6.9	9.0	23.8	10.8	7.4	4.3
Picoides canicapillus	China	97.0	63.6	81.9	17.0	5.6	6.8	18.6	8.6	5.5	3.3
Picoides cathpharius	China	103.4	79.3	86.4	19.0	5.9	7.4	19.1	9.2	5.9	3.7
Blythipicus pyrrhotis	China	144.5	106.1	140.4	44.8	12.0	12.9	32.5	18.0	9.7	6.5
Picus canus	China	147.0	123.7	152.5	38.3	10.0	11.7	31.5	15.9	9.7	6.7
Gecinulus grantia	China	159.3	122.7	178.5	41.9	10.8	11.4	33.9	16.9	10.9	6.7
Sasia africana	Africa	48.9	20.5	46.8	11.0	5.0	5.7	13.2	6.4	3.4	2.0
Campethera cailliautii	Africa	94.1	69.3	95.2	15.9	5.8	7.9	19.7	10.7	5.7	3.8
Campethera nivosa	Africa	81.8	52.5	76.0	16.9	6.3	7.9	20.2	10.3	5.5	3.4
Campethera caroli	Africa	101.1	70.3	94.9	23.1	7.4	9.2	21.7	12.3	6.9	4.5
Dendropicos xantholophos	Africa	111.0	81.3	98.8	29.3	8.5	9.7	24.4	11.0	7.1	4.7
Dendropicos elliottii	Africa	90.8	76.0	88.0	23.0	7.3	9.3	19.8	10.7	6.1	4.0
Picumnus rufiventris	Peru	62.8	35.1	61.1	17.5	6.0	7.6	19.2	10.4	4.6	3.0
Piculus chrysochloros	Peru	139.5	90.8	115.8	27.4	7.6	9.7	24.6	15.2	8.3	5.1
Piculus leucolaemus	Peru	116.9	79.1	101.9	22.7	7.4	9.9	22.0	12.8	7.4	4.6
Celeus grammicus	Peru	126.7	90.1	104.4	22.5	7.8	10.6	25.3	13.9	7.1	4.9
Celeus flavus	Peru	139.4	101.9	128.0	25.7	8.5	10.9	31.4	15.9	8.6	5.7
Celeus torquatus	Peru	153.7	116.1	146.5	34.1	8.5	10.4	29.2	17.1	9.3	6.5
Celeus elegans	Peru	153.9	111.3	148.6	30.6	10.0	12.6	32.2	17.4	9.5	6.5
Melanerpes cruentatus	Peru	108.1	70.0	98.0	23.5	6.7	9.1	21.6	12.3	5.9	4.2
Veniliornis affinis	Peru	95.5	67.1	80.6	22.1	6.6	9.3	20.2	11.1	6.2	4.1
Dryocopus lineatus	Peru	201.7	151.0	180.0	42.0	12.2	14.4	38.1	20.9	12.1	8.5
Campephilus melanoleucos	Peru	186.7	140.4	171.6	46.1	12.9	15.7	39.6	18.8	13.0	8.3
Campephilus rubricollis	Peru	187.8	142.1	166.3	45.6	11.7	16.1	41.9	19.7	12.3	8.1

each species to a class. Three of the seven species from the Minnesota assemblage were included in the original classification. These are the species for which ecological analyses were conducted (*Dryocopus pileatus, Picoides villosus,* and *Picoides pubescens*). The ecology of the remaining four species (*Melanerpes carolinus, Melanerpes erythrocephalus, Sphyrapicus varius,*

and *Colaptes auratus*) as well as most of the species from the European assemblage is sufficiently well-known to include in the original classification. However, they were left unclassified in order to test the predictive capabilities of the DFA.

Although independence of data is not a specific assumption of DFA, the analysis can be influenced by multicollinearity (McGarigal et al. 2000). Using the factor scores from Principal Components Analysis eliminates this problem, but can reduce the discriminatory power of DFA (McGarigal et al. 2000). Therefore, both the log-transformed measurements and the first four factor scores from PCA were analyzed separately. A consensus approach was then used to determine classification. If a species was identified as the same type (either "conventional" or "novel") in both analyses, then it was classified accordingly. If, however, the analyses assigned two different classifications to a species (e.g. the species was classified as "conventional" with the analysis of the log-transformed variables, and "novel" with the analysis of factor scores), then the species was classified as "undetermined."

Results

Ecology

Of the ecological variables analyzed, perch diameter explained the most variation in the data, followed by microhabitat and foraging maneuver (Table 2.6 and 2.7, Figures 2.3 and 2.4). Several Malaysian woodpeckers used smaller perches than woodpeckers from the other sites, and some tropical woodpeckers from both the Malaysian and Guatemalan sites used atypical microhabitats, such as bamboo and arboreal ant nests, with high frequency (Figures 2.3 and 2.4). In general, most woodpecker species used similar foraging maneuvers regardless of microhabitat, with the exception of a few Guatemalan species that foraged frequently on fruit.

Morphology

Body size accounted for most of the variation in the data (96%; Table 2.8), with the smallest species being *Sasia abnormis* (Malaysia) and the largest species being *Mulleripicus pulverulentus* (Malaysia). The second principal component indicated an inverse relationship between tail length and toe length (3%). When the data set of regressed variables was analyzed, bill size explained most of the variation. An inverse relationship between tail (along with wing and tarsus length) and toe length also accounted for a large amount of variation (26%) (Table 2.9). Plots of the factor scores reveal that, with the exception of one Malaysian species (*Sasia abnormis*), woodpeckers from all sites exhibited a similar range of body sizes; however, body "shape" differed between the woodpeckers from Maryland and Minnesota and the two tropical sites: birds from the temperate sites tended to have relatively long tails, short toes, and large bills (Figures 2.5 and 2.6), whereas some of the species from the tropical sites deviated from that shape to some degree (either by having relatively small bills, or relatively short tails and long toes, or a combination).

Correlating Ecology with Morphology

Canonical Correlation Analysis revealed a correlation between body size and perch diameter, with small woodpeckers using small perches and large species using large perches while foraging (Tables 2.10 and 2.11, and Figure 2.7). When the effects of body size were removed (with the regressed variables), there was a correlation between shape and microhabitat, (Tables 2.13 and 2.14), with relatively long-tailed, short-toed, big-billed woodpeckers foraging primarily on dead and live wood, and short-tailed, long-toed / short billed woodpeckers using more 'novel' microhabitats such as rattan, leaves, or fruit.

Canonical Redundancy Analysis of the log-transformed morphological data and the ecological data set (including perch class) revealed that morphology (i.e., body size) was a good predictor of ecology (perch diameter) with 78% of the variation in morphology for the first canonical variable explaining 74% of the variation in ecology. However, only 33% of the variation in ecology in the first canonical variable explained 32% of the variation in morphology (Table 2.12). Canonical Redundancy Analysis of the regressed variables and ecological data (without perch class) revealed predictive power in both sets of variables. The ecological data set was (microhabitat) slightly better at predicting morphology (shape), with 33% of the variation in ecology for the first canonical variable explaining 25% of the variation in morphology, and 25% of the variation in morphology in the first canonical variable explaining 19% of the variation in ecology (Table 2.15). This variation in predictive power may occur because the shape effect was confined to small to medium-sized species. Therefore, body size, to some degree can predict microhabitat (i.e., very large birds use large perches, but also invariably use "conventional" microhabitats).

Classifying Ecomorphs

Discriminate Function Analysis was able to classify the temperate and tropical ecomorphs of woodpeckers with a high probability of correctness. The original jackknifed classification matrix had a probability of 95% for the log-transformed data and 90% for the factor scores from PCA. These percentages mean that species were classified correctly with an 90-95% probability. After species from the additional assemblages were classified by DFA, the probabilities changed little (95% and 90% for the log-transformed and factor scores data respectively) (Table 2.16).

All species from the temperate zone assemblages were classified as "conventional," whereas approximately half the species from tropical assemblages were classified as "novel." Five species were assigned as "undetermined" because of conflicting results in the two analyses (*Piculus chrysochloros, Celeus elegans, Melanerpes pucherani, Melanerpes aurifrons*, and *Dendropicos elliotii*) (Table 2.16). Interestingly, these "problem" species came only from the tropical assemblages and perhaps reflect intermediate morphology.

Table 2.6. Partial contributions of foraging variables to each dimension. Numbers represent the proportion of variation in the dimensions explained by each variable.

Substrate/method	Dimension 1 (34%)	Dimension 2 (17%)	Dimension 3 (12%)
EXAT	0.07	0.16	0.05
EXL	0.03	0.01	0.05
EXD	0.10	0.00	0.12
GAT	0.02	0.12	0.08
GL	0.10	0.14	0.03
GD	0.00	0.01	0.06
GLEAF	0.03	0.01	0.00
PL	0.01	0.13	0.08
PD	0.00	0.13	0.11
PLEAF	0.01	0.00	0.00
PBROM	0.01	0.02	0.00
FL	0.00	0.09	0.04
FD	0.00	0.01	0.00
Perch			
XS	0.20	0.02	0.18
S	0.10	0.04	0.00
M	0.02	0.00	0.19
L	0.11	0.01	0.00
XL	0.20	0.10	0.00

Discussion

A distinct morphology was detected that is associated with some species of tropical woodpeckers. Generally, these species tended to exhibit one or a combination, of the following two shape characteristics (in comparison to the temperate woodpeckers): (1) relatively short tails, wings, and tarsi, and relatively long toes, or (2) relatively small bills. These "novel"

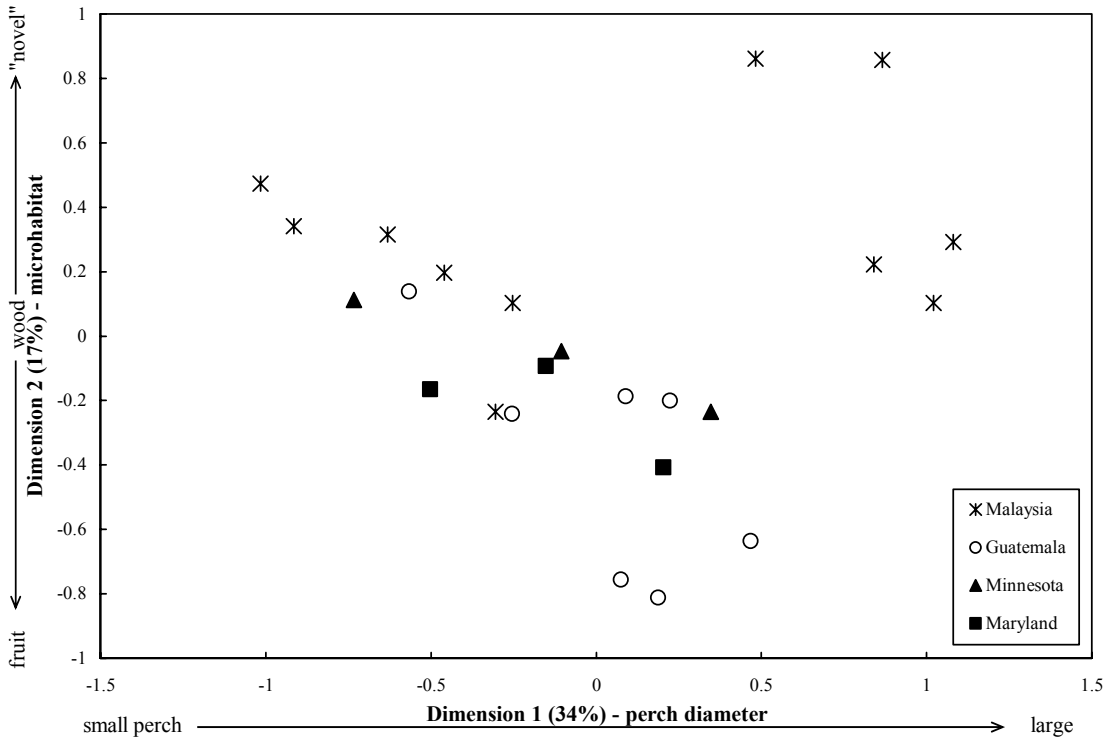


Figure 2.3. Correspondence plot of foraging variables. Dimension 1 represents the range of perch diameters used, and dimension 2 represents the range of microhabitats used.

woodpeckers tended to forage on microhabitats other than wood and were not typically oriented on these microhabitats in "conventional" woodpecker fashion with the tail used as a brace and the feet as clasps. Instead, the feet were often used in a more typical "perching bird" manner, with both feet clamped around the substrate. Also, the tail was rarely used as a brace. Even the species that excavated frequently continued to orient on microhabitats in the atypical configuration described above such that the bird often delivered blows from a sideways position rather than head on.

For these "conventional" woodpeckers, ants were a primary food source. In Malaysia, three woodpeckers (*Celeus brachyurus, Meiglyptes tristis*, and *Meiglyptes tukki*) were observed

Table 2.7. Partial contributions of foraging variables (without perch diameter) to the dimensions. Numbers represent the proportion of variation in dimensions explained by each variable.

Variable	Dimension 1 (36%)	Dimension 2 (22%)	Dimension 3 (14%)
EXAT	0.26	0.00	0.29
EXL	0.04	0.01	0.05
EXD	0.11	0.27	0.01
GAT	0.13	0.00	0.28
GL	0.29	0.00	0.25
GD	0.01	0.00	0.00
GLEAF	0.05	0.02	0.05
PL	0.01	0.29	0.00
PD	0.04	0.24	0.00
PLEAF	0.01	0.00	0.04
PBROM	0.00	0.03	0.01
FL	0.04	0.12	0.03
FD	0.00	0.01	0.00

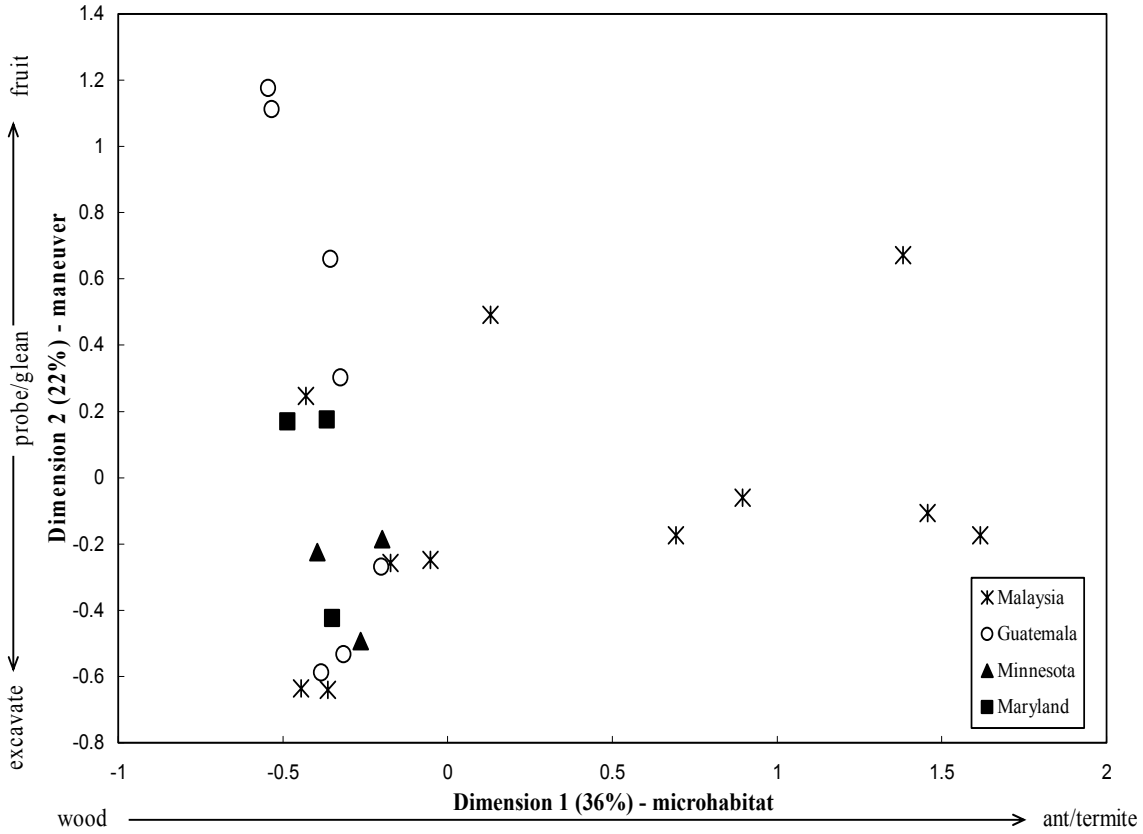


Figure 2.4. Correspondence plot of foraging variables (without perch). Dimension 1 represents the range of microhabitats used, and dimension 2 represents the range of foraging maneuvers used.

Table 2.8. Component loadings of log-transformed morphometric measurements. The high (> 0.50) positive loadings on PC1 indicates that most of the variation in the data is due to body size. The fairly high (> =/- 0.30) loadings on for tail length, and to a lesser degree, toe length (negative) on PC2 indicate an inverse relationship between tail and toe length.

Measurement	PC 1 (96%)	PC 2 (3%)	PC 3 (0.7%)
Wing	0.99	0.12	-0.07
Tail	0.95	0.31	-0.03
Body	0.99	0.08	-0.09
Culmen	0.98	-0.06	0.12
Bill Height	0.97	-0.19	0.05
Bill Width	0.98	-0.16	0.07
Tarsus	0.99	0.10	0.04
Toe 2	0.95	-0.27	-0.16
Width - Toe nail 2	0.99	0.05	0.07
Height - Toe nail 2	1.00	0.01	0.00

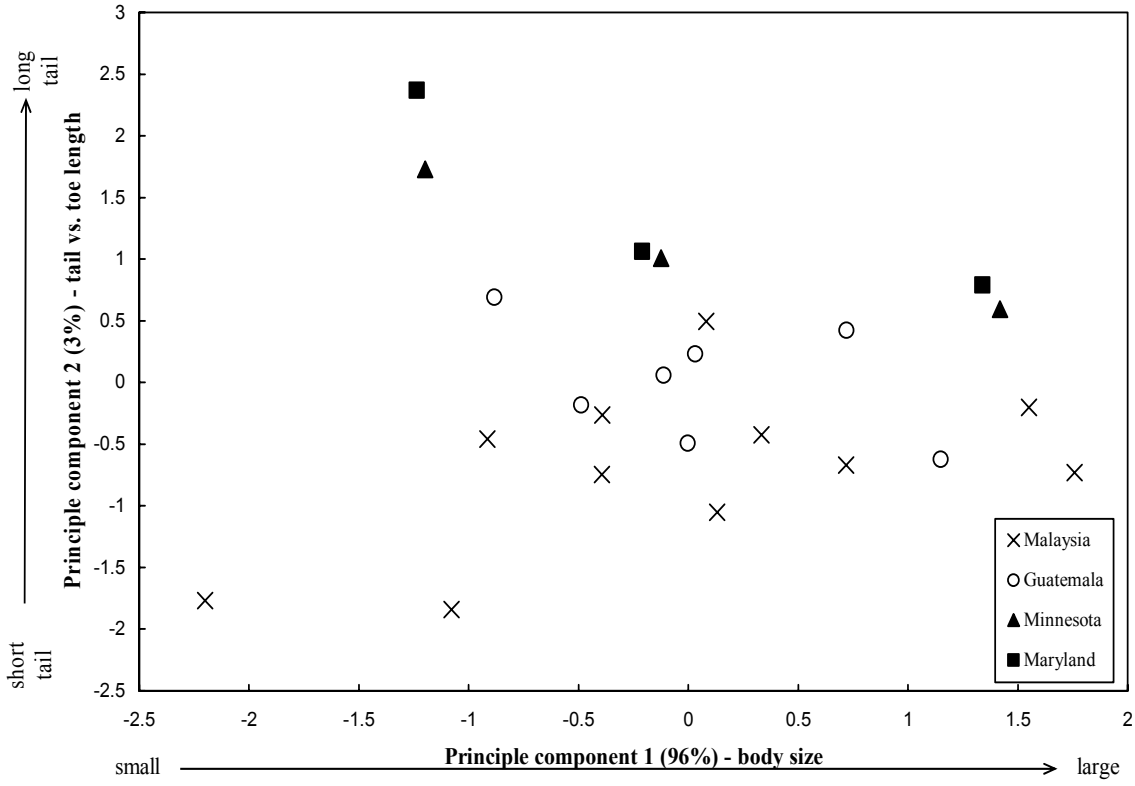


Figure 2.5. Plot of factor scores of Principal Components Analysis of log-transformed measurements. The X axis represents the range of body sizes and the Y axis represents the distribution of shapes (tail length).

Table 2.9. Component loadings of the log-transformed measurements regressed against body size. The high loadings (> +/- 0.30) on PC1 indicate an inverse relationship between tail length and all measurements except wing length. The high (> +/- 0.50) loadings indicate an inverse relationship among several variables (tail, tarsus, wing, and toe nail width vs. toe length).

Residuals	PC 1 (49%)	PC 2 (26%)	PC 3 (10%)
Wing	0.02	0.61	0.73
Tail	-0.35	0.86	-0.15
Culmen	0.81	0.16	0.29
Bill Height	0.86	-0.32	0.15
Bill Width	0.90	-0.09	0.00
Tarsus	0.51	0.66	0.01
Toe 2	0.67	-0.58	0.14
Width - toe 2	0.75	0.50	-0.33
Height - Toe 2	0.85	0.23	-0.33

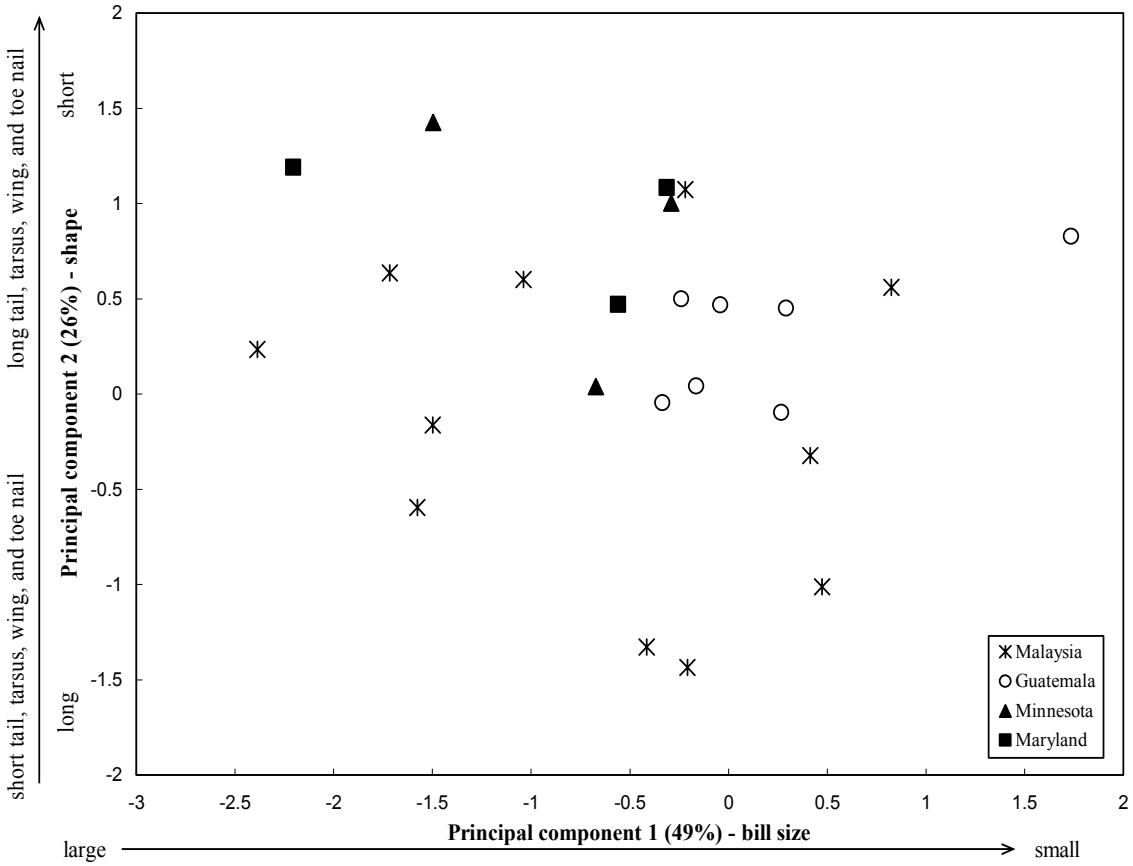


Figure 2.6. Plot of factor scores from Principal Components Analysis of regressed variables. The X axis represents the range of bill sizes, and secondarily, tail lengths. The Y axis in the inverse relationship between toe length and tail, tarsus, wing, toe nail width).

Table 2.10. Canonical Correlation Analysis – log transformed data. Canonical variables, eigen values, and individual and cumulative proportions of the variation explained by the canonical variables. F tests are of the hypothesis that the canonical variable in the given row and all that follow is zero.

Variable	Eigenvalue	Proportion	Cumulative	F Value	DF	Pr > F
1	20.1	0.9	0.9	3.8	30	0.0002
2	2.2	0.1	1.0	1.2	18	0.3134
3	0.2	0.0	1.0	0.3	13	0.9659

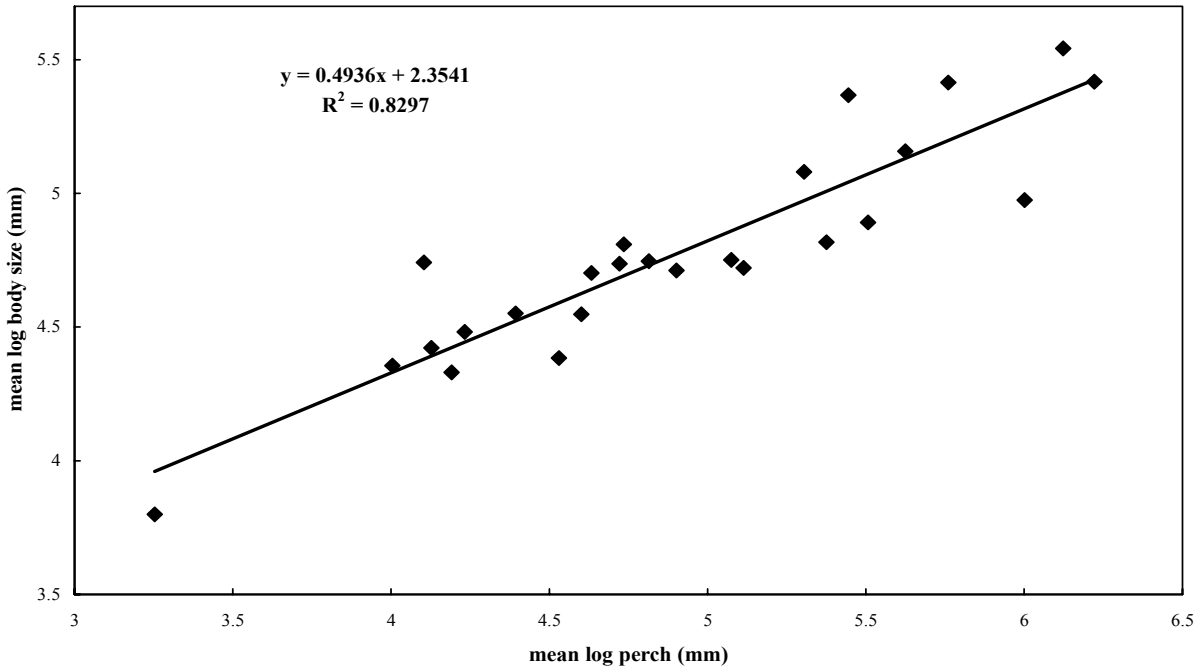


Figure 2.7. Plot of mean log perch diameter and mean log body sizes.

foraging on ant nests suspended in vegetation on numerous occasions. The birds typically perched either on top of the nest itself or hung from a branch around which the nest was built. Foraging involved short bursts of tapping or pecking followed by frenzied feeding. The woodpeckers would forage until covered with ants, at which point they would leave the nest for a nearby branch to remove the ants (by wing beating and preening); then, they would return to the nest to continue foraging. This process would continue until the nest was completely

demolished. These tropical woodpeckers were also seen foraging on ant galleries or chambers along trees branches, lianas, rattan, palms, and bamboo. Such galleries are made by ants from several genera including the genus *Crematogaster* (Holldobler and Wilson 1990).

Table 2.11. Correlations between the morphological measurements and ecological measurements with their own and the opposite canonical variables (log-transformed data). M = morphological canonical variables, E = ecological canonical variables.

	M1	M2	M3	E1	E2	E3
Wing	0.89	0.06	0.19	0.87	0.05	0.07
Tail	0.89	-0.01	0.16	0.87	-0.01	0.06
Body	0.88	0.13	0.25	0.86	0.12	0.10
Culmen	0.92	0.09	0.16	0.89	0.08	0.06
Bill height	0.86	0.27	0.21	0.84	0.22	0.08
Bill width	0.85	0.21	0.18	0.83	0.17	0.07
Tarsus	0.94	0.02	0.17	0.92	0.02	0.07
Toe 2	0.77	0.19	0.41	0.75	0.15	0.15
W – Toe nail 2	0.92	0.12	0.19	0.90	0.10	0.07
H – Toe nail 2	0.90	0.12	0.25	0.87	0.10	0.09
D 1 (perch)	-0.96	0.06	0.05	-0.99	0.08	0.14
D 2 (microhabitat)	0.07	0.82	-0.03	0.07	0.10	0.07
D 3 (maneuver)	0.14	0.05	0.37	0.14	0.06	0.99

Table 2.12 a. Canonical Redundancy Analysis – ecological measurements (log-transformed data). Proportions of variation in the ecological data explained by the ecological canonical variables, and by the morphological canonical variables.

	Ecological Canonical Variables			Morphological Canonical Variables	
Variable No.	Proportion	Cumulative Proportion	R-Square	Proportion	Cumulative Proportion
1	0.33	0.33	0.95	0.32	0.32
2	0.33	0.67	0.68	0.23	0.55
3	0.33	1.00	0.14	0.05	0.59

Table 2.12 b. Canonical Redundancy Analysis – morphological measurements (log-transformed data). Proportions of variation in the morphological data explained by the morphological canonical variables, and by the ecological canonical variables.

	Morphological Canonical Variables			Ecological Canonical Variables	
Variable Number	Proportion	Cumulative Proportion	R-Square	Proportion	Cumulative Proportion
1	0.78	0.78	0.95	0.74	0.74
2	0.02	0.80	0.68	0.01	0.76
3	0.05	0.85	0.14	0.01	0.76

Table 2.13. Canonical Correlation Analysis – regressed data. Canonical variables, eigen values, individual and cumulative proportion of the variation explained by the canonical variables, and F test of the hypotheses that the canonical variable in the given row and all that follow is zero.

Variable	Eigen value	Proportion	Cumulative	F Value	DF	Pr > F
1	3.4	0.7	0.7	1.9	27	0.0335
2	1.4	0.3	0.9	1.3	16	0.2938
3	0.3	0.1	1.0	0.6	7	0.7172

Table 2.14. Correlations between the morphological measurements and ecological measurements with their own and the opposite canonical variables (regressed data). M = morphological canonical variable, E = ecological canonical variable.

	M1	M2	M3	E1	E2	E3
Wing	0.61	-0.38	-0.15	0.53	-0.29	-0.07
Tail	0.78	0.02	0.09	0.69	0.01	0.04
Culmen	0.32	-0.06	-0.28	0.28	-0.05	-0.14
Bill height	-0.09	0.28	-0.04	-0.08	0.21	-0.02
Bill width	0.19	0.32	0.11	0.171	0.24	0.05
Tarsus	0.66	-0.24	-0.42	0.58	-0.18	-0.20
Toe 2	-0.31	-0.15	0.38	-0.28	-0.11	0.19
W – Toe nail 2	0.65	0.36	-0.12	0.57	0.28	-0.06
H – Toe nail 2	0.36	0.17	-0.09	0.32	0.13	-0.05
D1 (microhabitat)	-0.65	0.41	0.20	-0.74	0.54	0.41
D2 (maneuver)	-0.13	-0.55	0.34	-0.15	-0.72	0.68
D3 (combination)	0.58	0.34	0.30	0.66	0.45	0.61

Table 2.15 a. Canonical Redundancy Analysis – ecological measurements (regressed data). Proportions of variation in the ecological data explained by the ecological canonical variables, and by the morphological canonical variables.

	Ecological Canonical Variables			Morphological Canonical Variables	
Variable Number	Proportion	Cumulative Proportion	R-Square	Proportion	Cumulative Proportion
1	0.33	0.33	0.77	0.26	0.26
2	0.33	0.67	0.58	0.19	0.45
3	0.33	1.00	0.24	0.08	0.53

Table 2.15 b. Canonical Redundancy Analysis – morphological measurements (regressed data). Proportions of variation in the morphological data explained by the morphological canonical variables, and by the ecological canonical variables.

	Morphological Canonical Variables			Ecological Canonical Variables	
Variable Number	Proportion	Cumulative Proportion	R-Square	Proportion	Cumulative Proportion
1	0.25	0.25	0.77	0.19	0.19
2	0.06	0.31	0.58	0.04	0.23
3	0.05	0.36	0.24	0.01	0.24

Table 2.16. Classification of species based on Discriminate Function Analysis. Percentages underneath species indicated as "Undetermined" are probabilities that the species was classified correctly, and (log) and (pca) indicates the analysis. Con. = conventional and Nov. = novel.

Region	Conventional	Novel	Undetermined	Con.	Nov.	Total
Malaysia	*Blythipicus rubiginosus*	*Sasia abnormis*				
	Picus mentalis	*Hemicircus concretus*				
	Picus puniceus	*Meiglyptes tristis*				
	Dinopium rafflesii	*Meiglyptes tukki*				
	Reinwardtipicus validus	*Celeus brachyurus*				
	Dryocopus javensis	*Picus miniaceus*				
	Mulleripicus pulverulentus			**7**	**6**	**13**
Guatemala	*Veniliornis fumigatus*	*Piculus rubiginosus*	*Melanerpes aurifrons*			
	Dryocopus lineatus	*Celeus castaneus*	**[71% typical (log)]**			
	Campephilus guatemalensis		**[57% tropical (pca)]**			
	Melanerpes pucherani			**4**	**2**	**7**
Peru	*Celeus torquatus*	*Picumnus rufiventris*	*Piculus chrysochloros*			
	Dryocopus lineatus	*Melanerpes cruentatus*	**[74% typical (log)]**			
	Campephilus melanoleucos	*Veniliornis affinis*	**[74% tropical (pca)]**			
	Campephilus rubricollis	*Piculus leucolaemus*				
		Celeus grammicus				
		Celeus flavus				
		Celeus elegans		**4**	**7**	**12**
Gabon	*Dendropicos xanthologus*	*Sasia africana*				
		Campethera cailliautii				
		Campethera nivosa				
		Campethera caroli				
		Dendropicos elliotii		**1**	**5**	**6**
China	*Picoides hypertherius*					
	Picoides canicapillus					
	Picoides cathpharius					
	Blythipicus pyrrhotis					
	Picus canus					
	Gecinulus grantia			**6**	**0**	**6**
Minnesota	*Picoides pubescens*					
	Picoides villosus					
	Melanerpes carolinus					
	Melanerpes erythrocephalus					
	Sphyrapicus varius					
	Colaptes auratus					
	Dryocopus pileatus			**7**	**0**	**7**
Germany	*Picoides major*					
	Picoides leucotos					
	Picoides medius					
	Picoides minor					
	Dryocopus martius					
	Picus canus			**6**	**0**	**6**

Species that frequently used bamboo (primarily *Sasia abnormis*) usually foraged at specific parts of bamboo, most notably nodes or junctions from which bamboo runners extended. When disturbed by the observer, ants typically emerged from these nodes. Dransfield (1981a) observed ants nesting between the culm-sheaths and blades of young culm shoots and branch shoots of *Dinochloa trichogona* in Sabah, and bamboo-ant associations have been documented in the Neotropics (Wheeler 1942).

One species in particular, *Meiglyptes tristis* (Buff-rumped Woodpecker), foraged frequently on leaves, a novel foraging behavior for a woodpecker. On occasions when the observer could get a good view of the leaves where birds were foraging (either with binoculars, or by examining the leaves in hand if they were low enough), there were usually small ant nests or chambers at the base of the leaves (see also Wells 1999). This species also frequently foraged on the leaves and tips of *Macaranga* trees, and two other species (*Meiglyptes tukki* and *Celeus brachyurus*) were observed foraging on the branch tips (but not the leaves) of *Macaranga*. These trees have mutualistic associations with ants (genus *Crematogaster*), and disturbing the leaves and tips of the branches causes these ants to emerge. Woodpeckers were also seen foraging on rattans with known ant associations (genus *Daemonorops*; Ickes personal comm.). On numerous occasions, woodpeckers were observed foraging on lianas and epiphytes where ants were swarming. Whether these were actual ant-plants (e.g. several genera in the family Asclepiadaceae; Merrill 1981) is unknown, but the foraging tactic of these woodpeckers was similar to that described for arboreal ant nests.

In Neotropical forests, fruit is also an important resource for woodpeckers. However, several species in both Neotropical (e.g. several species in the genus *Celeus*) and Tropical African forests (some *Campethera* species) are known to forage frequently on arboreal ant nests

(Haverschmidt 1958, Hilty and Brown 1986, Kilham 1979, Short 1982, Slud 1964, Wetmore 1968), and at least one Neotropical species (*Celeus spectabilis*) is known to forage on ants found in bamboo (genus *Bambusa*; Kratter 1997).

Although some woodpecker species from tropical assemblages exhibited a distinct morphology related to a distinct ecology, variation is also considerable among the species of woodpeckers classified as "conventional." When DFA was conducted without the "novel" species, birds separated discretely into two classes: (1) birds with relatively large bills and long tails, and (2) species with slightly shorter tails and somewhat shorter bills (Table 2.17). This classification likely reflects a distinction between species that excavate frequently and those that forage in different ways (e.g. fruit and nut eating, ground foraging, frequent gleaning, and occasional sallying).

Table 2.17. Classification of 'typical' woodpeckers based on Discriminate Function Analysis.

Region	Excavator	Other	Ex.	Oth.	Total
Malaysia	*Dinopium rafflesii*	*Blythipicus rubiginosus*			
	Reinwardtipicus validus	*Picus mentalis*			
	Dryocopus javensis	*Picus puniceus*			
	Mulleripicus pulverulentus		**4**	**3**	**7**
Guatemala	*Dryocopus lineatus*	*Veniliornis fumigatus*			
	Campephilus guatemalensis		**2**	**1**	**3**
Peru	*Dryocopus lineatus*	*Celeus torquatus*			
	Campephilus melanoleucos				
	Campephilus rubricollis		**3**	**1**	**4**
Gabon		*Dendropicos xantholophus*	**0**	**1**	**1**
China	*Picus canus*	*Picoides hypertherius*			
	Gecinulus grantia	*Picoides canicapillus*			
		Picoides cathpharius			
		Blythipicus pyrrhotis	**2**	**4**	**6**
Minnesota	*Picoides villosus*	*Picoides pubescens*			
	Dryocopus pileatus	*Melanerpes carolinus*			
		Melanerpes erythrocephalus			
		Sphyrapicus varius			
		Colaptes auratus	**2**	**5**	**7**
Europe	*Picoides major*	*Picoides medius*			
	Picoides leucotos	*Picoides minor*			
	Dryocopus martius	*Picus canus*	**3**	**3**	**6**

This study supports the idea that the "additional" woodpecker diversity seen in tropical rainforests is to some degree related to their specialization on microhabitats not available in temperate forests. However, tropical woodpeckers are necessarily more specialized than temperate species. When comparing species from Guatemala to those in Maryland and Minnesota, Askins (1983) suggested that an increased diversity of resources was important in explaining diversity in the Guatemalan assemblage. By comparing the degree of specialization and overlap of resource use in birds from the Guatemala site to those from the temperate sites, the study predicted that birds from the more diverse Guatemalan assemblage would exhibit either increased specialization or increased overlap in resource use compared to the birds from the temperate sites. The lack of significant differences in specialization or resource overlap between the Guatemalan and temperate assemblages suggested that the higher diversity was related to an increase in the resource base rather than increased specialization.

When the data collected in Malaysia were compared to data from Guatemala, Maryland, and Minnesota, there was a similar result (Figures 2.8 and 2.9). Malaysian birds were significantly broader in their use of foraging heights from all sites, and more specialized in the range of perch diameters used compared to the Maryland assemblage. However, mean specialization or niche breadth was not significantly different. On the other hand, Malaysian species exhibited significantly less overlap in comparison to all other sites ($p < 0.001$ for Guatemala, $p = 0.05$ for Maryland, and $p = 0.02$ for Minnesota). Most of this difference was due to less overlap in perch diameters used by the Malaysian birds, but there was also significantly less overlap in foraging height for the Malaysian birds compared to the Guatemalan birds. These results are opposite of the predictions that would explain diversity, and suggest an increased resource base.

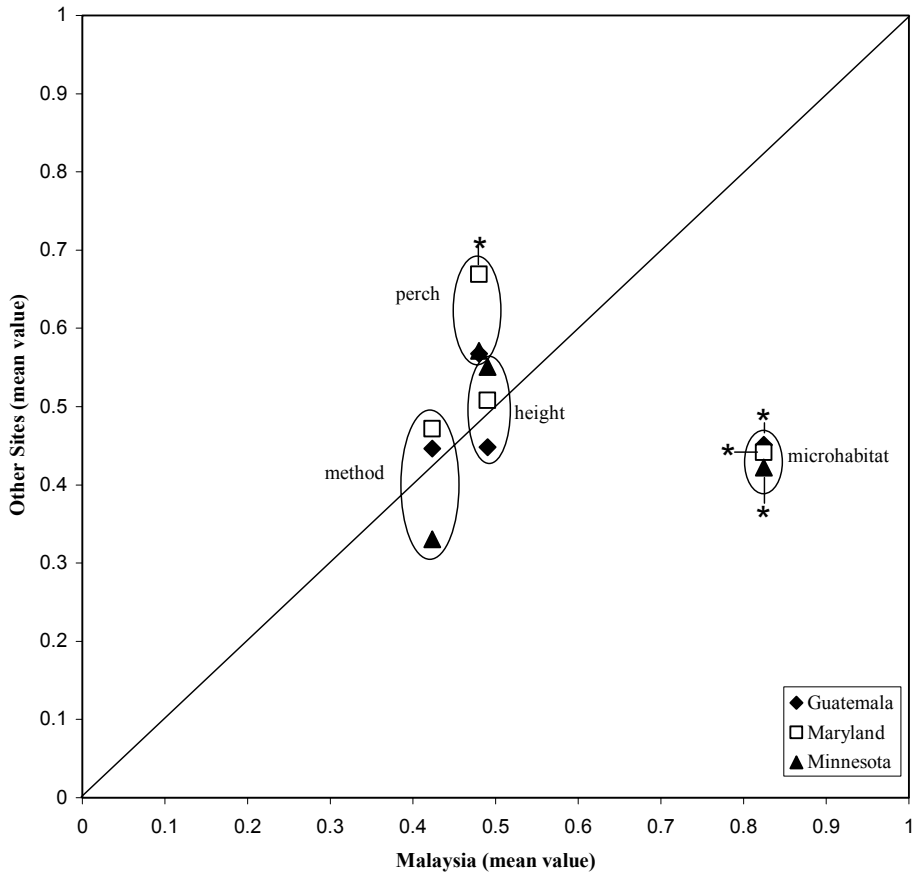


Figure 2.8. Mean niche breadths for four foraging parameters. Asterisks indicate comparisons that are significantly different for a given parameter.

The problem with these predictions is that they rely on the principals of competitive exclusion and limiting-similarity in the communities, which are difficult to prove unequivocally. Fortunately, one need not assume competition and its related predictions to see that woodpeckers in the tropical assemblages are using additional resources. The correspondence analyses revealed an extension of the microhabitats and foraging maneuvers used by woodpeckers from both tropical assemblages and an extension of the size of perches used by the Malaysian woodpeckers (smaller perches) (Figures 2.3 and 2.4). Likewise, the tropical woodpeckers, although similar in their range of sizes, exhibited a broader range of shapes compared to the temperate woodpeckers (Figures 2.5 and 2.6). This difference in shape (which was correlated

with microhabitat use) was also detected in other tropical assemblages (Peru and Gabon), but not in any of the other temperate assemblages studied (Europe, China, and the remaining species from the Minnesota assemblage; Table 2.16).

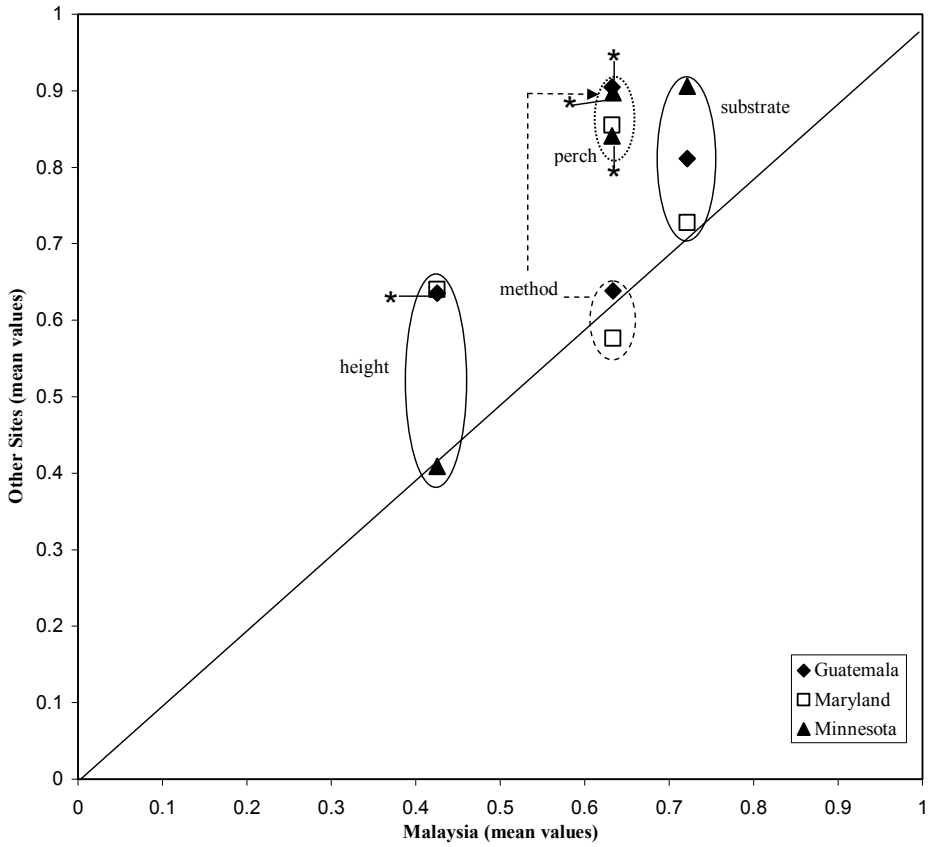


Figure 2.9. Mean niche overlaps for four foraging parameters. Asterisks indicate comparisons that are significantly different for a given parameter.

The presence of "additional" resources and related "additional" diversity in tropical ecosystems has been quantitatively shown in numerous studies in the Neotropics. Some of these resources included bamboo (Kratter 1997), dead leaves (Rosenberg 1997), bromeliads (Sillett 1997), and army ants (Willis and Oniki 1983). These studies were different from this one in that they approached the issue of "additional" diversity from the side of the resource rather than the guild or assemblage (this study, Askins 1983, and Remsen 1990). Many of the species that were

specialized on these 'tropical' resources had no close relatives in temperate regions. Although a few woodpecker species are known to specialize on a specific 'tropical' resource such as bamboo (*Gecinulus viridus* – the Bamboo Woodpecker, *Celeus spectabilis* – the Rufous-headed Woodpecker), none of the species I studied was restricted to a single microhabitat. The dietary preferences of the "novel" woodpeckers were likely very similar, however, and consisted primarily of ants and termites. The "conventional" species in the assemblage obtained ants primarily from trees either by excavating deep into wood, probing into crevices and between vines and lianas wrapped around trees, gleaning three surfaces, or ripping apart epiphytes. The "novel" species on the other hand, exhibited similar foraging maneuvers, but obtained ants from resources not typically found in temperate systems such as arboreal carton nests, or ants associated closely with plants such as rattans, bamboo, lianas, and the branch tips and leaves of certain trees.

Ants and termites are extremely diverse and abundant in tropical forests (Collins 1989, Wilson 1987), and can be found at all levels of the forest (Abe 1979, Bruhl et al. 1998). Ants in particular are particularly specialized to certain forest strata, and often specific plant taxa (Bruhl 1998, Dransfield 1981b, Merrill 1981, Wheeler 1942). Understanding diversity in these ant and termite communities may lend insight into the processes that maintain woodpecker diversity in tropical forests.

CHAPTER 4
SUMMARY - TROPICAL WOODPECKER DIVERSITY: ECOLOGICAL INSIGHTS AND PRACTICAL CONCERNS

Introduction

Woodpeckers are a well-known group of birds with distinctive physical, behavioral, and plumage characteristics. Their unique specializations allow them to excavate hard substances for food and nesting space. Thus, in the habitats where they occur, woodpeckers form not only a distinct taxon, but also a discrete ecological guild. Because of their close associations with forests, and because they create nest cavities that are used by a suite of other species, woodpeckers are often a focus of forest management (Conner et al. 1994, Flemming et al. 1999, Moorman et al 1999, Welsh and Capen 1992).

The goal of this study was to investigate patterns of diversity in woodpeckers to gain insight into causes of the maintenance of high diversity in tropical rainforests. Because of their distinct ecology and widespread distribution, woodpeckers are good model organisms for such studies. Woodpeckers, like many other bird species, reach their highest diversity in tropical rainforests. Although well-known in temperate forests, relatively few studies have focused on tropical woodpeckers (Askins 1983, Short 1970, 1973, 1974, 1978), and quantitative data on foraging ecology was non-existent. Field research was conducted in the lowland rainforests of Southeast Asia (Malaysia) where woodpeckers reach their highest within-habitat diversity (up to 16 species in a single patch of lowland rainforest). The foraging ecology of 13 species was studied to gain an understanding of coexistence within the guild and to use as a basis for a broader study in diversity.

The tropical lowland forests of Southeast Asia are under the increasing pressures of habitat loss and fragmentation. Although there is some debate on the role of managed forests in

conservation of wildlife (Bawa 1998, Chazdon 1998), sustainable forest management is considered by many to be an important aspect in the conservation of tropical forest species (Montagnini et al 2002, Noble and Dirzo 1997, Putz et al. 2001). Studies on the birds in selectively logged forests have documented a variety of changes to the bird community after logging (Johns 1989, Johns 1996, Lambert 1992, Wong 1985, 1986). Although there seems to be no single pattern of change after logging, generally a homogenizing effect between forests and surrounding habitats occurs as species not normally found in closed forest penetrate the forest interior while sensitive forest species become low in abundance or disappear (Bawa 1998, Lambert 2002). Some studies have suggested that woodpeckers are potentially sensitive to logging although data were lacking (Johns 1989, Lambert 1992). To address this issue, woodpecker surveys were conducted and important woodpecker microhabitats were sampled in logged and unlogged forests (see Chapter 1).

Study Findings: Ecological Explanations

Results from field observations indicate a broad array of foraging behaviors and microhabitat usage. One species, *Meiglyptes tristis*, frequently foraged on leaves, a behavior not documented in any other woodpecker species in the world. Despite this diversity in foraging ecology, woodpeckers could be characterized into two general groups: (1) "conventional" species that foraged on snags or parts of living trees (n = 6 species), and (2) "novel" species that used microhabitats such as arboreal ant and termite nests, bamboo, lianas, and rattans (n = 5 species; Chapter 1).

Ecomorphological analyses of the data collected in Malaysia, combined with a data set of observations from Guatemala, Maryland, and Minnesota, revealed that "conventional" species have relatively long tails, short toes, and large bills, whereas "novel" species had relatively short

tails, long toes and small bills. This "novel" ecomorph was found only in the tropical assemblages studied (n = 4), whereas the "conventional" ecomorph was found in all assemblages studied (n = 8; Chapter 2).

Study Findings: Practical Concerns

Response to Logging

Results from woodpecker surveys revealed an atypical response to logging. Typically, species either drop in abundance in recently logged forest and increase in older logged stands (the amount of increase varies among species), or become more abundant after logging and decrease in abundance in older logged stands. Woodpeckers, on the other hand, were slightly less abundant in recently logged forest (5-years-old), and much less abundant in older logged forest (10-years-old). This pattern suggests a time lag in the effects of logging on woodpeckers. Microhabitat samples showed that dead wood was abundant in recently logged forest, and much less abundant in the older logged forest. Perhaps this residual dead wood buffers woodpeckers temporarily from logging effects. As the residual decays, numbers also drop. Such a time lag has been documented in other studies of woodpeckers in disturbed habitats (Ligon and Stacey 1996, Ripper unpubl. data, Martin personal comm.).

Despite the variety of foraging preferences and microhabitats used by Malaysian woodpeckers, snags were the resource most in demand in all forest types, and the large snag-foraging species may be particularly vulnerable. *Mulleripicus pulverulentus* in particular seems to be tied to an abundance of snags and is absent from older logged stands (up to 45 years). Studies have suggested that snags are less abundant in tropical forests than temperate forests, and thus may be an important focus for management (Gibbs et al. 1993, Pattanvibool and Edge 1996).

Conservation/Management Issues

Woodpeckers as Focus Species

A recent review of published and unpublished research throughout the Sunda region including data from Styring (2001, unpubl. data) indicated that all forest woodpecker species are likely at risk from logging and fragmentation (Lambert 2002). Woodpeckers constitute 13% of the species for which evidence of negative impacts is definitive. The response of woodpeckers to logging was not uniform, but many species exhibited similar responses to other sensitive bird species such as babblers (Timaliidae), understory flycatchers (Muscicapidae), and trogons (Trogonidae). For example, understory species in general are considered at risk to logging, although not all understory species exhibit similar responses to logging. *Picus mentalis,* an understory woodpecker that prefers areas with little understory vegetation (Lammertink 2001), is uncommon in recently logged forest with thick understory. As logged stands age and the understory becomes more open, *P. mentalis* numbers increase. They may even become more abundant in old logged forest with a homogeneously clear understory than in primary forest that is more heterogeneous (see Chapter 1). This open understory is also a microhabitat preferred by certain insectivores such as trogons, flycatchers, and some babblers (*Malacopteron*). Two other understory woodpeckers, *Sasia abnormis* and *Blythipicus rubiginosus,* preferred areas of dense vegetation, a microhabitat also preferred by babblers in the genera *Stachyris* and *Macronous*. Finally, two other understory woodpeckers used microhabitats such snags or logs (*Reinwardtipicus validus*), or palms/rattans (*Meiglyptes tukki*). This preference for specific food sources in the understory may be important to many sensitive understory birds; however, little quantitative research has been conducted on the foraging ecology or habitat preferences of Southeast Asian species.

Unlike the understory woodpeckers discussed, the large woodpeckers studied (*Dryocopus javensis* and *Mulleripicus pulverulentus*) showed strong preferences for areas with abundances of snags (Lindenmayer et al. 1999). This fact, combined with research indicating that snags are less abundant in tropical forests than in temperate forests (Gibbs et al 1993, Pattanvibool and Edge 1996), suggests snags should be a management consideration.

The Importance of Sustainable Forestry

Although selective logging can have a significant impact on bird populations, it is considered less damaging than habitat conversion (Lambert 2002). Even when forests are converted to "bird-friendly" plantations such as *Albizia* (Mitra and Sheldon 1993) or agroforests (Thiollay 1995), the effect is greater than logging (Table 3.1). In Malaysia, the most common plantation type, oil palm, has not been well studied, most likely because it contains very few bird species, and most of which do not frequent the rainforest interior.

Reasons for why areas designated for logging may be converted to plantation are: (1) Arrested or delayed regeneration. This lack of regeneration occurs when there is significant damage during logging (due to excessive tree removal, destructive extraction practices, or poor road planning). The resulting erosion and overgrowth of grassy vegetation can slow or even stop regeneration (Bawa 1998, Chazdon 1998, Putz et al 2000, 2001) (2) Limited regeneration of economically valuable species. This problem occurs when too many large seed trees are removed from a stand, or when conditions in the logged stand discourage the regeneration of valuable species (Uuttera et al. 2000). (3) Human degradation. Logging roads increase access to people, who often further degrade the area with slash and burn farming, illegal logging, and hunting (Jepson et al. 2001, Robinson et al. 1999). (4) Fire. When a rainforest is logged, light is allowed to penetrate the forest floor and dry out debris. Dead wood left behind also dries out and

becomes fuel, and surrounding fires from nearby agriculture may ignite the forest (Cochrane et al 1999, Cochrane and Laurance 2002, Cochrane and Schulze, Woods 1989, Kinnaird and O'Brian 1998, Uhl 1998, 1998). This drying effect is increased with increased light penetration (i.e. increased canopy damage). Although primary rainforest is buffered from fire, the drier logged forest is susceptible. It has been found that once a stand of forest burns, the chances increase that it may burn again (Cochrane et al 1999), and repeated burning turns forest to grass and shrub-land (Woods 1989). Few studies have looked at bird abundances in burned, logged forest. Preliminary data from a burned site in Brunei suggests low woodpecker abundance and diversity (Table 3.1). This is possibly a worst-case scenario, because the area that burned was peat swamp, and the peat itself likely smoldered for a considerable amount of time.

Although conversion has more impact than logging, fragmentation is the most severe threat to many tropical rainforest birds (Brookes et al. 1999, Lambert 2002, Laurance et al. 2001). Species found in logged forest and even in agroforest, such as *Meiglyptes tristis*, are negatively affected by fragmentation (Table 3.1; Lambert 2002). Singapore, with only a small fragment of primary forest (50 ha) remaining, surrounded by second growth (1400 ha), serves as an example for the region. Of the 12 forest woodpecker species that occurred in Singapore, nine are extinct and two are of uncertain status (Table 3.1). The species lost included large and small woodpeckers as well as species apparently tolerant to logging and some types of habitat conversion.

Conversion of logged forest is an important cause of fragmentation. However, logging practices in and of themselves can cause degradation and eventual fragmentation of adjacent patches of primary forest. When fire occurs in logged forest, it may penetrate primary forest to some degree (Wood 1989). If these areas of both logged and primary burned forest are

increasingly susceptible to fire, then the amount of true primary forest may gradually dwindle. A similar process may occur when logging roads are poorly constructed, and prevent canopy regeneration. The road is essentially an edge that exposes the primary forest to harsh conditions such as wind and erosion. Damage caused on this edge may eventually reduce the size of the primary forest fragment as the forest edge shifts inward (Gascon et al. 2000). A study in Borneo uncovered complex interactions between logging, mast fruiting, and seed predation (Curran et al. 1999). Complete recruitment failure occurred within a primary forest inside a National Park surrounded by logged forest. This recruitment failure was due to intense seed predation by Bearded Pigs (*Sus barbatus*) (Curran et al. 1999). Mast fruiting in this region is believed to be an adaptive response to seed predators, but if logging decreases availability of seeds, then predator satiation may not occur. If such recruitment failure occurs over several mast fruiting events, then forests may begin to senesce, and results in increased fragmentation and degradation.

These problems associated with logged forests illustrate the careful planning that needs to occur before every logging event. Loss of timber-producing forest should be of equal concern to forest managers. In Malaysia, some beneficial management practices are already in place, such as the establishment of small protected areas (called Virgin Jungle Reserves) in every forest reserve. Also considerable research and development is underway on reduced-impact extraction techniques (helicopter and cable logging). However, these techniques are not yet in wide use. High-tech solutions may not be more effective than careful planning and use of skilled workers. Sustainable forest management can likely be achieved through a combination of carefully considered cutting limits (with additional consideration to "overmature" or dead trees and whether diameter limits actually create desired results), longer stand rotations (research suggests

at least 70 years), well-planned construction of logging roads, and, perhaps most importantly, careful extraction of logs (Putz et al. 2000, 2001). Snag creation management, whereby a given number of trees per hectare are killed approximately 10 years after logging, may also be a useful consideration. This investment is one that can benefit forest and wildlife managers, as well as conservationists, and local people whose economy stands to benefit from forests that are rich in a variety of resources.

Table 3.1. Summary of the effects of different types habitat disturbance on woodpeckers. Data comes from Lambert 1993 (primary, log 10-15), Mitra and Sheldon 1993 (primary, *Albizia*), Thiollay 1995 (primary, Hevia, Damar, Durian), Styring and Ickes 2001 (primary, log 25+), Styring Chapter 1 (Primary, Log < 9, and Log 10 -15), and Styring unpubl. data (log burn, abandon). An x represents percentages of the total sample in increments of ten (x > 1-10 %, xx > 10 -20%, etc.). Log burn was forest of undetermined age (likely logged around 15 + years before study) that was burned approximately 5 years before the study. *Albizia*, *Hevia*, Damar, and Durian are different types of plantation. Abandon was an abandoned fruit plantation (time since abandonment not determined). Under the Singapore column E indicates a species that is extinct in Singapore, U indicates that the status of the species is uncertain, and N indicates a species that has never been documented on Singapore. A † indicates a species for which there unambiguous evidence that it is sensitive to fragmentation (Lambert 2002). A ‡ indicates a species for which there is unambiguous evidence of negative response to both fragmentation and logging (Lambert 2002). A * indicates a species that is considered Near-threatened by BirdLife International.

Species	**Primary**	**Log < 9**	**Log 10-15**	**Log 25+**	**Log burn**	***Albizia***	***Hevia***	**Damar**	**Durian**	**Abandon**	**Singapore**
Sasia abnormis	xxx	xxx	xx	x	-	-	x	x	x	-	N
Hemicircus concretus†	xx	x	xx	xx	-	xx	xx	-	-	x	**E**
Meiglyptes tristis†	xx	xx	xx	xx	-	xx	-	xx	-	xx	**E**
Meiglyptes tukki‡*	xxxx	x	x	xxxx	-	-	xx	xx	-	-	**E**
Celeus brachyurus†	xx	xx	-	xx	x	xx	x	x	x	x	**P**
Blythipicus rubiginosus‡*	xxxx	xxxx	xxx	xx	-	-	-	-	-	-	**E**
Picus puniceus‡	xxx	xx	x	xxxx	-	-	x	-	-	-	**E**
Picus mentalis‡	xxxx	x	xxx	xxxxxx	-	-	-	-	-	-	**E**
Picus miniaceus†	xx	xxxx	-	xxxx	-	-	-	xx	-	-	**P**
Dinopium rafflesii†*	xxx	xx	xx	-	-	-	-	-	-	-	**E**
Reinwardtipicus validus†	xxxxxx	x	xx	xx	-	-	xx	-	-	-	**E**
Dryocopus javensis†	xxxxx	xxx	x	xx	x	-	-	-	-	-	**U**
Mulleripicus pulverulentus†	xxxx	xxx	-	-	x	-	-	-	-	-	**E**

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VITA

Alison R. Styring was born to Dr. Theodore R. and Dina F. Robinson on February 24, 1972, in Baton Rouge, Louisiana. Her family moved to Gainesville, Georgia, in July 1977, and she lived there until 1990 when she was graduated from Gainesville High School and moved to Bloomington to attended Indiana University. Although she had always enjoyed the outdoors, it was during her college career that Alison became increasingly interested in ecology. During this time, Alison worked at Yellowstone National Park and traveled to Australia where she became fascinated with its unique fauna. Alison received a Bachelor of Arts degree in biology in 1994 and returned to Australia in 1995 to live with the family of her fiancé Matthew Styring. Alison and Matt were married in September 1996 in Gainesville, and they moved to Baton Rouge the following August when Alison began graduate school at LSU. She will receive the degree of Doctor of Philosophy at the December 2002 commencement.